MONARCH BUTTERFLY (Danaus plexippus) BREEDING DISTRIBUTION AND HABITAT PREFERENCES IN SOUTHEASTERN ONTARIO

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ABSTRACT

Habitat loss is considered a strong driver of the decline of the eastern migratory population of the North American monarch butterfly (*Danaus plexippus*). While research has focused on the loss of suitable habitats in agricultural areas in the American Midwest, little is known about monarch breeding habitat preferences at the northern limits of its summer range in Canada. I first conducted a literature review on monarch habitat preferences and population dynamics across its North American range and on the role of community science in the monitoring of spatial dynamics. Seventeen years of community science records (n=5461) reporting the presence of butterfly species in southeastern Ontario were then used to compare land covers and spatial attributes of butterfly records that included the monarch with records that did not. The models indicate that the probability of observing monarchs, compared to other butterflies in this region, decreases going northward and westward, away from water bodies, and with increasing deciduous or needleleaf forest cover. Clusters of monarch observations (hot spots) are found north of Lake Ontario. Compared with cold spots where the probability of observing the monarch is low, the hot spots tend to have more shrubland and less deciduous forest and urban land cover. A field comparison of the vegetation at a subset of hot and cold sites identifies potential nectaring species at these latitudes, and compares how milkweed abundance, plant richness, and the diversity of potential nectaring plants drive habitat preferences. It offers some of the first evidence that, in this region, milkweed abundance may not be a limiting factor for monarch breeding habitat selection. It also shows a greater ecological gradient in potential nectaring species assemblages in hot spots than in cold ones, ranging from grassland species in conserved lands in the developed regions near Lake Ontario, to forest edge species and shrubs within rights of way in forested regions to the north. While the importance of preserving

monarch resources in agricultural landscapes has been acknowledged, the role of successional habitats in forested landscapes has been little considered. This research shows that preserving such spaces is an important feature of monarch conservation at the northern range edge. This study also demonstrates the value of community science data to delineate areas of conservation interest.

RÉSUMÉ

La perte d'habitat est considérée comme un facteur important du déclin de la population migratrice de l'Est du monarque nord-américain (*Danaus plexippus*). Alors que la recherche s’est concentrée sur la perte d'habitats propices dans les zones agricoles du Midwest américain, on en sait peu sur les préférences d'habitat du monarque à la limite nord de son aire de répartition estivale au Canada. J’ai d’abord effectué une revue de littérature sur les préférences d'habitat du monarque et la dynamique des populations dans l’ensemble de son aire de répartition en Amérique du Nord, ainsi que sur le rôle de la science communautaire dans le suivi des dynamiques spatiales. Dix-sept années de relevés scientifiques communautaires (n =5461) signalant la présence d’espèces de papillons dans le sud-est de l’Ontario ont ensuite été utilisés pour comparer les couvertures terrestres et les attributs spatiaux des listes d’observations de papillons qui incluaient le monarque avec les listes d’observations qui ne l’incluaient pas. Les modèles indiquent que la probabilité d’observer des monarques, comparativement à d’autres papillons dans cette région, diminue vers le nord et vers l’ouest, loin des plans d’eau et avec l’augmentation du couvert forestier de feuillus ou de conifères. Des concentrations d’observations de monarques (des points chauds) se trouvent au nord du lac Ontario. Par rapport aux points froids où la probabilité d’observer le monarque est faible, les points chauds ont tendance à avoir plus d’arbustes et moins de feuillus et de couverture terrestre urbaine. Une comparaison sur le terrain de la végétation dans un sous-ensemble de sites chauds et froids identifie les espèces nectarifères potentielles à ces latitudes et compare la façon dont l'abondance de l'asclépiade, la richesse des plantes et la diversité des plantes nectarifères potentielles déterminent les préférences en matière d'habitat. Ceci constitue l’une des premières preuves que, dans cette région, la disponibilité de l'asclépiade ne serait pas un facteur limitant pour la sélection de l'habitat de reproduction du monarque. Ceci montre également un plus grand gradient écologique dans les assemblages d’espèces nectarifères potentielles dans les points chauds que dans les points froids, allant des espèces de prairies dans les zones conservées des régions développées près du lac Ontario, aux espèces de lisière forestière et aux arbustes dans les emprises des régions boisées au nord. Bien que l’importance de préserver les ressources du monarque dans les paysages agricoles soit reconnue, le rôle des habitats de succession dans les paysages forestiers a été peu étudié. Cette recherche montre que la préservation de tels espaces pourrait être une caractéristique importante de la conservation du monarque à la limite nord de l'aire de répartition. Cette étude démontre également la valeur des données de science participative pour délimiter des zones d’intérêt pour la conservation.

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CONTRIBUTION TO ORIGINAL KNOWLEDGE

The results of this research represent the following developments:

1. Provide an original review of the current research on the ecology of the monarch butterfly, and the contribution of community science data to this research
2. Elucidate land cover preferences and spatial attributes for monarchs at the northern edge of their distribution in southeastern Ontario.
3. Map hot spots, clusters of monarch observations; and cold spots, where the probability of observing the monarch is low, in southeastern Ontario, and identify their respective characteristics.
4. Provide a list of potential nectaring plant species for the northeastern monarch region
5. Demonstrate the value of community science data to the study and conservation of monarchs.

CONTRIBUTION OF AUTHORS

This manuscript-based thesis represents original and independent work performed by Marian MacNair. CHAPTER 2 was written by Marian MacNair and edited by Dr. Sylvie de Blois. For CHAPTER 3, occurrence data were provided by Dr. Maxim Larrivée through the Montreal Insectarium. Marian MacNair designed the study, planned and executed the fieldwork, and conducted the analyses under the guidance of Dr. de Blois and Dr. Larrivée. Marian MacNair wrote the manuscript in CHAPTER 3, with Dr. de Blois contributing to the writing and editing, and Dr Larrivée contributing to the editing.

1 GENERAL INTRODUCTION

Monarch butterflies (*Danaus plexippus*) are charismatic mini-fauna: an icon of biodiversity conservation whose power and significance belie their tiny size (Gustafsson et al., 2015). Millions follow their spectacular and dangerous annual migration from summer breeding habitat as far north as southern Canada across North America to winter in central Mexico or southern California (Howard, 2018; Prudic, McFarland, Oliver, et al., 2017). The monarch has the power to change policy and practice across physical, national and mental boundaries, engaging people from differing organizations, cultures and countries.

The North American migratory populations have experienced precipitous declines in the last two decades (Brower et al., 2012; Rendón-Salinas et al., 2019). Research has pointed to changes in the overwintering sites, land development and changing agricultural practices in the breeding grounds and migratory pathways, as well as climate change, predation and invasive species all contributing to this decline (Agrawal & Inamine, 2018; Malcolm, 2018; Thogmartin, Wiederholt, et al., 2017). A massive effort from governments, associations and individuals has resulted in the conservation and restoration of habitat for monarchs and other pollinators across their range, while contributing to community science efforts and the identification and protection of overwintering and summer breeding sites (Thogmartin, Wiederholt, et al., 2017). Community science data from thousands of citizens across North-America allow tracking the monarch across its vast territory (Ries & Oberhauser, 2015; Silvertown, 2009). Researchers are coming to rely on this data, and to find statistical methods for compensating for its biases (Bird et al., 2014).

In spite of the attention monarchs have received, habitat preferences in their summer breeding ground and migration dynamics are still little understood, especially in the species' northern range. Eastern Canada is part of the northeastern (or north central in Flockhart, Brower, et al. (2017)), summer reproductive range of the monarch, and research shows this region can be an important and growing reservoir for the species (Flockhart, Brower, et al., 2017). Yet little is known about monarchs' habits and preferences at northern latitudes, and how climate change may affect their distribution and requirements. This thesis attempts to establish where they are found in southeastern Ontario and what their land cover and breeding habitat preferences are in this region.

1.1 OBJECTIVES

1. Identify land cover and spatial attributes related to monarch occurrence during their summer breeding season at the regional level.
2. Identify and map clusters of sites where the probability of observing monarchs is high, i.e., 'hot spots', and compare their land cover and habitat features to those of 'cold spots' in the region.
3. Construct a list of potential nectaring plants for the northeastern monarch region and compare the milkweed and nectaring plant species' availability in hot and cold spots in the field.

1.2 HYPOTHESES

Because of their dependence on milkweed for breeding, we expect monarchs to be observed less in forests than in other more open habitats, with an abundance of milkweed and nectaring species being distinctive features of hot spots.

2 LITERATURE REVIEW

2.1 Monarch biology and ecology

2.1.1 Taxonomy and description

The monarch butterfly is believed to be named in honor of King William III of England, also titled the Prince of Orange (Adams, 1992). Orange and black monarch butterflies are morphologically distinct, though the Viceroy (*Limenitis archippus*) is a mimic (Ackerly & Vane-Wright, 1984; Center for Biological Diversity [CBD] et al., 2014; Finkbeiner et al., 2018; Oberhauser & Solensky, 2004)

Monarchs are members of the family *Nymphalidae*, known as brushfoot butterflies for the hairs on their front legs. Monarchs belong to the subfamily *Danaianae*, or milkweed butterflies, as they oviposit only on plants in the *Asclepiadoideae* subfamily of the *Apocynaceae* (dogbane), in the genus *Asclepias* and related genera (CBD, 2014; Traut et al., 2017).

2.1.2 Distribution

Though they are not genetically distinct (Zhan et al., 2011), two North American populations of migratory monarchs are divided by the Rocky mountains into eastern and western breeding areas, migration routes, and winter roosts. These range from southern Canada to Mexico and the Caribbean. Non-migratory populations also exist in southern Florida and the Caribbean. Introduced populations exist in such areas as Hawaii, Australia and New Zealand (Agrawal, 2017; CBD, 2014). This research focusses on the summer northeastern breeding population of the migratory monarch east of the Rockies that overwinters in Mexico.

2.1.3 Life history

Each summer female monarchs oviposit on milkweed plants. Caterpillars hatch after 3-6 days and feed on the milkweed host, growing through several instars, the periods between molting. The caterpillar forms a chrysalis which ecloses to a butterfly after 13-21 days (Urquhart, 1960). Summer breeding adults live 2-5 weeks, (Zalucki, 1983; Zalucki et al., 2016) feeding on nectar, mating and laying the next generation (Zalucki et al., 2016). Three to six generations can occur in a year (Howard, 2018; Oberhauser & Solensky, 2004; Zalucki & Kitching, 1984).

2.1.4 Migration and overwintering

From their overwintering site in Mexico (Urquhart & Urquhart, 1976), four generations commonly disperse north to reach southern Canada (Batalden et al., 2007; Inamine et al., 2016). Geographic and climate variables predict monarch breeding occurrence across 12 million km^2 in models (Flockhart et al., 2013). Though most monarchs will migrate only to the lower U.S. in the first stage (Malcolm, 2018), and successive generations disperse north, some adults will sweep across the breeding range (Miller et al., 2012). This research project examines the last two generations near their northern extent.

The final generation, termed 'Methuselahs,' fly up to 4000km back to Mexico to overwinter in massive clusters in oyamel fir trees (*Abies religiosa*) in a mountainous area of central Mexico (Brower, 1996; Rendón-Salinas et al., 2019; Urquhart & Urquhart, 1976). Temperature and humidity conditions here allow the butterflies to maintain low body temperatures to conserve lipids through the winter, when nectaring resources are scarce (Brower et al., 2006; Masters et al., 1988). This aggregation also allows researchers to monitor changes in the population size (Malcolm, 2018).

These same butterflies then mate and migrate north to breeding grounds and lay the first generation of the new cycle (Malcolm, 2018; Miller et al., 2012; Pitman et al., 2018). The eastern population, which migrates longer distances than western monarchs, have larger and more angular forewings (Altizer & Davis, 2010; Flockhart, Fitz-Gerald, et al., 2017).

Though much remains to be learned about how monarchs navigate across succeeding generations (Mouritsen, 2018; Oberhauser et al., 2013), monarchs use daylight and magnetic cues to find their way (Reppert et al., 2010; Reppert et al., 2016). Temperature may play a role in triggering migration (Guerra & Reppert, 2015). Recent research suggests they may also use scent cues to find sites (McNeil, 2021). Favourable wind currents may also aid migration (Stefanescu et al., 2007). Migration pathways may reach a choke point at the Gulf of Mexico (Knight, Harrison et al.), where migratory populations of different origins mix. Early migration benefits females, while males are more likely to suffer mortality during the southward migration and overwintering (Steffy, 2015).

The majority of the overwintering population (up to 58%) originates from the Midwest U.S. in most years, though northeastern and north central populations can contribute substantial proportions (Flockhart, Brower, et al., 2017; Oberhauser et al., 2017; Wassenaar & Hobson, 1998). Regional climate on the breeding ground appears to most influence these origins (Flockhart, Brower, et al., 2017; Inamine et al., 2016; White & Kerr, 2007). New methods, such as plotting changes in butterfly population dynamics using genomics, museum specimens, and radio-telemetry tracking, are being developed (Flockhart et al., 2015; Ryan et al., 2018; Steffy, 2015; Wilcox et al., 2021).

2.1.5 Land cover and habitat preferences

2.1.5.1 Temperature and humidity

Climate and temperature conditions have a strong effect on butterfly populations (Aardema et al., 2011; Bladon et al., 2020; Kesler, 2019; Zalucki, 1982). The amount of precipitation and diurnal temperature range are key requirements (Oberhauser & Peterson, 2003).

High spring precipitation and average temperatures in Texas result in large population growth in Ohio (Zipkin et al., 2012).

Heat waves and drought can negatively affect larvae (James, 2016). Humidity has been demonstrated to be important for butterflies and bumblebees (Gupta et al., 2019; Harrap et al., 2021). Maintaining humid grasslands and milkweed patches in moist locations is recommended (James, 2016; Kati et al., 2012), although monarchs are observed to avoid large water bodies (Urquhart, 1960). The presence of water or humid conditions could therefore predict monarch occurrence.

2.1.5.2 Land cover

Though some milkweed species are strongly affected by land cover, the latter is not always an indicator for monarch occurrence, as research indicates monarchs are generalists who can make use of diverse habitats (Bhowmik, 1994; Hartzler, 2010; Pleasants & Oberhauser, 2013; Zalucki & Rochester, 2004; Zaya et al., 2017). They exhibit preferences for certain open habitats, such as grasslands, wetlands and croplands, where nectaring plants can bloom (Ackerly & Vane-Wright, 1984; Kesler, 2019; Kral et al., 2018). Research points also to a preference for oviposition in row crop habitats (Myers et al., 2019) and rural roadsides (Hellerstein et al., 2017; Kasten et al., 2016), while butterflies in south Germany exhibited a preference for early successional fields with abundant flowers (Steffan-Dewenter & Tscharntke, 1997).

The context of these open habitats has also been shown to be important in some landscapes, but not in others. Surrounding forest cover, for instance, showed a strong positive effect on butterfly species richness in Swedish grasslands (Bergman et al., 2018), but not in Colorado (Collinge et al., 2003). In Iowa, monarchs were shown to avoid large amounts of canopy cover (Dinsmore et al., 2019).

Recent research points to the importance of preserving large areas of undisturbed habitat for conservation (Mokany et al., 2020). This thesis seeks to establish whether land cover can predict monarch occurrence in their northeastern breeding region. The study area contains large urban areas, agricultural land north of Lake Ontario grading to less disturbed forested land to the north. This provides an opportunity to examine where monarchs are found or flourish in a region with such diverse land covers.

2.1.5.2.1 Urban land cover and gardens

Urbanization can have a negative effect on the Lepidoptera and pollinators in general (Bates et al., 2011; Bergerot et al., 2011; Blair, 1999; Deguines, 2012; Di Mauro et al., 2007; Theodorou et al., 2020). Declining habitat quality and limited habitat in the surrounding landscape negatively affects species richness and abundance (Olivier et al., 2016), especially in peri-urban landscapes (Radeloff et al., 2005).

When evaluating urban areas for conservation, scientists are impeded by their lack of familiarity with distinctive or critical factors in urban landscapes (Lizée et al., 2016; Parker, 2015). Except for the distance to other sites, conservation value cannot always be predicted by geographic or site characteristics (Fattorini, 2014). Moreover, the value of urban green spaces is questioned because they host ubiquitous and alien species. But it is important to establish value based on all the species actually present.

In urbanizing areas of medium anthropogenic pressure, the richest habitat in both butterfly species and number of individuals is fallow lands, followed by gardens, while vineyards and forests host poorer communities (Lizée et al., 2011). Fallow lands are in decline in some regions. Proximity to natural, forested areas increases butterfly diversity in a tropical urban landscape (Koh & Sodhi, 2004). Overall biodiversity was found to be comparable between urban green spaces and intensively-managed agricultural areas (Turrini & Knop, 2015). At higher urban densities, guarding existing natural area was most valuable for increasing butterfly populations. However, at lower levels of urbanization, planting new gardens resulted in the highest population sizes (Soga et al., 2014).

Urban gardens were found to increase landscape permeability and improve colonization for butterflies (Coristine et al., 2016). Butterfly gardens have increased butterfly population sizes in tropical regions (Mathew & Anto, 2007). The amount of sunlight and floral resource abundance was the best predictor of pollinator diversity in urban landscapes (Matteson & Langellotto, 2010), suggesting roof-top gardens may be effective (Wang et al., 2017). Larger patch area and habitat heterogeneity increased species richness (Matthies et al., 2017; Tonietto et al., 2011), as did limited management for butterfly species richness (Sing et al., 2016). Generalist pollinator species did better in residential areas with exotic flowers than specialist bee species, who were limited to natural parks (Threlfall et al., 2015). The study area for this thesis includes the large urban areas of Toronto and south Ottawa, which contain urban gardens and naturalized public areas. Are fewer monarchs observed in these urban areas than in rural regions?

Planted milkweed areas in urban and residential gardens can have higher monarch egg densities than those found in natural areas (Cutting & Tallamy, 2015; Nail et al., 2015; Stenoien et al., 2015). Baker and Potter (2019) found that juvenile density increased in gardens with spatially isolated milkweed compared to gardens with an admixture of milkweed and other plants. More eggs and larvae were also found in gardens having an access oriented poleward, and unimpeded by structures (Baker & Potter, 2019). Other studies found no differences in pollinator preferences (Harrison & Winfree, 2015).

The heterogeneity of urban gardens may increase butterfly community diversity (Lizée et al., 2011). Plant species richness was higher in neighbourhoods with racially or ethnically mixed human populations than homogenous populations cultivating fewer plant species (Lowenstein & Minor, 2016). Plant species varied between neighbourhoods, suggesting a disparity in ecosystem services across an urban environment (Matteson et al., 2013).

Gardening practices affect survival, but research is uncertain: a heavily-weeded garden without leaf litter may have fewer refuges for caterpillars from predators such as ants (Karban et al., 2013), but a weedy, complex garden may provide more habitat for predators and parasites (Langellotto & Denno, 2004; Majewska et al., 2018). Promoting milkweed in farmland does not necessarily increase weed cover (Martin et al., 2021).

2.1.5.3 Milkweed and the matrix

A flying insect such as a monarch uses multiple spatial scales, from landscape to local micro-environment, to determine where to alight; patch area, shape, connectivity, fragmentation and habitat heterogeneity have all been shown to influence a monarch's decision (Davis et al., 2007; Dilts et al., 2019; Pitman et al., 2018).

Habitat suitability for breeding monarchs is determined primarily by the presence of suitable habitat for milkweed, the host plant, and its climactic requirements (Dilts et al., 2019). It takes an average of 28.5 milkweed ramets to produce one migratory monarch butterfly from the north central U.S. (Stenoien et al., 2016). Monarchs in the Midwest prefer swamp (*A. incarnata)* and common milkweed (*A. syriaca)* (Pocius et al., 2018). Common milkweed is an opportunistic species found in many open habitats, while swamp milkweed prefers more humid areas (Bhowmik & Bandeen, 1976).

Phenology is synchronized between butterfly and plant, as milkweed developmental stage is important for egg-laying (Posledovich et al., 2018). Females typically oviposit a single egg per plant (Zalucki & Kitching, 1982b) on the underside of a leaf (Urquhart, 1960). Caterpillars accumulate toxins from eating the milkweed sap, which renders larval and adult monarchs unpalatable to predators (Bargar et al., 2020; Brower et al., 1984; Weitemier et al., 2019; Woodson, 1954).

Though availability of host plants has been shown to influence population size in some butterfly populations (Krauss et al., 2004), monarchs do not always show a preference for more milkweed or greater nectar availability (Kral et al., 2018; Zalucki 1987). Monarch females are effective milkweed hunters in large areas (Zalucki & Rochester, 2004). There is evidence that low density patches of suitable plants in an inhospitable matrix of agriculture or urban land cover are vital to monarch butterflies (Dennis & Hardy, 2007; Dennis, 2004; Zalucki & Kitching, 1982a; Zalucki & Lammers, 2010). The highest egg density was found in small, low-density milkweed patches in agricultural landscapes (Pitman et al., 2018), whereas natural areas tend to have lower egg densities than smaller sites with fewer milkweed plants, such as gardens (Stenoien et al., 2015). However, high egg density in smaller habitat patches within agricultural areas or gardens can also increase larvae competition; larvae tend to be smaller and weigh less at higher densities (Flockhart et al., 2012).

Reducing the availability of milkweed patches on the landscape, ‘cleaning up the matrix’, resulted in a 30% reduction in egg-laying (Stenoien et al., 2016; Zalucki et al., 2016). This emphasizes the importance of habitat corridors or connections (Dennis et al., 2013). Small, diverse patches within 250-1000m may increase butterfly diversity (Perović et al., 2015). Many small habitat patches, or so-called ‘nature strips’ within the monarch’s perceptual range may be more successful than large clusters of habitat widely dispersed across the landscape (Grant et al., 2018; Stenoien et al., 2016; Zalucki et al., 2016). This suggests an important role for garden patches in an urban matrix.

Monarch eggs and larvae were more abundant when milkweed was spread out around the edge, rather than in a patch (Baker & Potter, 2019). Females laid more eggs on milkweed in the open than surrounded by grasses of equal height. Grassland butterflies were shown to also prefer that patches be surrounded by diverse land use (Perović et al., 2015) and did better in humid landscapes with hedgerows and tree lines (Kati et al., 2012). Adult monarch abundance increased at sites with higher plant diversity (Kral-O'Brien et al., 2020). This project will attempt to discover if monarch habitat preferences in this northern region conform to the literature.

2.1.5.4 Nectar and other variables

Milkweeds, thistles (*Cirsium spp*.) and blazing stars (*Liatris spp*.), which may contain ideal nectar concentrations (Pivnick & McNeil, 1985), are important nectar resources for monarchs (Antonsen et al., 2021; Geest et al., 2018). In a monarch and pollinator seed mix, *A. syriaca* was the most observed species, though *A. tuberosa* and *A. incarnata* occurred at greater densities when planted (Lukens et al., 2020). Southern monarchs prefer informative flowers with floral cues, such as pattern and dimension (Esmaile & Rodrigues, 2020). Monarchs have been shown to use and even prefer exotic plants (Majewska et al., 2018), perhaps due to more showy flowers or greater nectar resources. Davis, Debinski et al. (2007) found that the percentage of litter was the most highly correlated with butterfly community composition.

2.1.5.5 Rights of way

Research indicates that rights of way on roadsides, hedgerows or power lines (ROW) could have conservation potential for monarchs, especially if other historical habitats are scarce

(Forrester et al., 2005; Kasten et al., 2016). Monarchs change their movement patterns to respond to ROW (Fjellstad, 1998), and high-quality breeding and nectaring habitat is available in these locations (Cariveau et al., 2020). Egg per plant densities are lower in ROW than other areas (Pitman et al., 2018). The surrounding land cover may be important: hedgerows in agricultural areas with smaller crop fields with lower crop diversity and more annual crops contained more milkweed (Martin et al., 2021). Late season mowing of fields and roadsides may increase resources for monarch larvae (Alcock et al., 2016; Cariveau et al., 2020; Fischer et al., 2015).

2.2 Monarch population dynamics

Tiny creatures of a few grams, with wings like sails on their back, monarch butterflies face many hazards. Population numbers can fluctuate by an order of magnitude from year to year (Rendón-Salinas et al., 2019; Semmens et al., 2016). Generally, fluctuations in these numbers are caused by abiotic factors such as unseasonal temperatures, storms or drought (Brower et al., 2004; Flockhart, Brower, et al., 2017; Stenoien et al., 2015; Zalucki & Rochester, 2004).

Population estimates for eastern population in the winter of 1996-1997 put the number at one billion butterflies. But less than 20 years later, numbers had fallen to fewer than 35 million, a decline of 97 percent (CBD, 2014). The western population has fared even worse in recent years (Pelton et al., 2019). On average, the migratory population of the monarch has declined by more than 84% in North America between 1993 and 2015 (Agrawal, 2019; Brower et al., 2012; Jepsen et al., 2015; Pleasants & Oberhauser, 2013; Rendón-Salinas et al., 2019; Saunders et al., 2019). These declining numbers, the small current population size and the large stochasticity of the monarch result in an 11–57% probability of quasi-extinction of the migratory population over the next 20 years, although uncertainty in these estimates is large (Semmens et al., 2016).

In response to these declines, the U.S. Fish and Wildlife Service (USFWS) was asked to list the monarch as a threatened species (CBD, 2014; Jepsen et al., 2015; Thogmartin, Wiederholt, et al., 2017). The Canadian government lists the monarch as of 'Special Interest' (Government of Canada, 2011). This research supports governments' attempts to learn more about monarch distribution and preferences here in Canada.

2.2.1 Monarch threats

This monarch decline has been attributed to multiple causes; degradation of the overwintering site, habitat loss due to changing agricultural practices and land development, hazards during migration and the threat of predation, parasites, invasive species and climate change (Agrawal, 2019; Agrawal & Inamine, 2018; Inamine et al., 2016; Malcolm, 2018; Wilcox et al., 2019). This reduction is also part of a global decline in insect and pollinator numbers (Biesmeijer et al., 2006). The loss of these pollination services will have negative ecological and economic impacts on species biodiversity, food security and ecosystem stability (Potts et al., 2010). Determining land cover and habitat preferences in southeastern Ontario may provide insight to assist conservation of the migratory population.

2.2.1.1 Overwintering hazards

Deforestation and degradation of the monarch's overwintering site are major threats (Agrawal, 2019; Brower et al., 2016; Navarrete et al., 2011; Ramírez et al., 2007; Thogmartin, Wiederholt, et al., 2017). The 2020 murder of rangers in the park at one of the over-wintering sites, potentially over illegal logging, suggests these threats may be increasing (British Broadcasting Corporation [BBC], 2020). Unfortunately, as the monarchs decline, the amount of forest required for overwintering and the incentive to protect the forest also declines.

2.2.1.2 Habitat Loss

Because monarchs prefer to oviposit on young milkweed (Bergström et al., 1994; Urquhart, 1987), historical changes to natural landcover may not have been detrimental for monarchs initially. For example, colonial deforestation for agriculture and indigenous burning regimes may have increased suitable open habitat for monarchs (Haan & Landis, 2019; Stenoien et al., 2015). The subsequent intensification of land use practices across North America, however, has been detrimental to the species. Monarch abundance was shown to be more than four times as sensitive to various perturbations on breeding grounds than at the overwintering sites (Flockhart et al., 2014).

2.2.1.2.1 Agriculture

Changing agricultural practices in the Midwest and north central U.S., the most productive birthplace of overwintering monarchs, have had a negative effect on monarch reproduction success (Flockhart et al., 2014; Pleasants et al., 2017; Saunders et al., 2018; Vane-Wright, 1993). Agriculture in these areas is now dominated by intensively-farmed, herbicide-tolerant corn and soybean fields (Martin et al., 2021; Tyler et al., 2015), which host less milkweed than smaller fields with more hedgerows (Martin et al., 2021). Almost all (92% and 94%, respectively) corn and soybean crops grown in the U.S. are now treated with herbicides preventing milkweed (Fernandez-Cornejo, 2015; Semmens et al., 2018).

The milkweed limitation hypothesis links the reduction of milkweed in agricultural land cover to the decline of monarchs (Malcolm, 2018; Saunders et al., 2018; Stenoien et al., 2016). Estimates of the number of milkweed lost in these areas range from 88% to 97% between 1999 and 2012 (Pleasants & Oberhauser, 2013). As many as 860 million milkweed ramets are estimated to have been eliminated from agroecosystems in the Midwest during this period

(Pleasants et al., 2017; Thogmartin, Diffendorfer, et al., 2017). This change has been rapid and directional, leading the monarch population to shift to remnant milkweed (Stenoien et al., 2016). This loss of field milkweed has been shown in simulations to reduce monarch fecundity – the number of eggs a female can lay in her lifetime (Ramírez et al., 2007; Zalucki & Lammers, 2010; Zalucki et al., 2016).

Other chemical inputs, such as neonicotinoid insecticides, have also been implicated in monarch declines (Forister et al., 2016; James, 2019; Olaya-Arenas et al., 2020; Samson-Robert et al., 2014; Tracy et al., 2019). Insecticides commonly used for mosquito control have devastated monarch larvae and adults, especially on migration routes (Oberhauser et al., 2006; Oberhauser et al., 2009; Thogmartin, Wiederholt, et al., 2017).

2.2.1.2.2 Land use change

Monarch numbers continued to decline even after herbicide use stabilized, implying the loss of milkweed in agriculture fields was not the only threat (Agrawal, 2019). Habitat loss is a leading cause of biodiversity loss globally (Pitman et al., 2018). Resource removal and habitat fragmentation from anthropogenic impacts such as land development may be reducing the general population throughout the range (Malcolm, 2018; Marini & Zalucki, 2017; Oberhauser et al., 2017; Radeloff et al., 2005; Stenoien et al., 2016; Thogmartin, Wiederholt, et al., 2017; Zalucki & Lammers, 2010; Zalucki et al., 2016). This fragmentation of habitat reduces the likelihood monarchs can disperse across a matrix empty of resources to the next suitable habitat (Coristine et al., 2016; Fernández-Chacón et al., 2014).

Urbanization is found to be the most detrimental land-use change for flower visitors and butterflies (Deguines, 2012; Olivier et al., 2016; Ramírez-Restrepo & MacGregor-Fors, 2017; Theodorou et al., 2020). The resulting reduction of floral nectar available to fuel migration and breeding (Brower et al., 2015; Brower et al., 2006; Saunders et al., 2018), and the reduction of certain species of milkweed (Boyle et al., 2019) has been implicated in the decline (Inamine et al., 2016). Urban gardens may compensate in part for the loss of resources, but there is also some evidence that urban gardens could serve as ‘ecological traps’ by enticing pollinators away from natural habitats and exposing them to predation, infection or pesticides (Levy & Connor, 2004; Majewska et al., 2018).

Fire suppression and lack of disturbance in old fields, parks and conservation areas may be limiting available resources for monarchs by allowing succession from open habitats to forest (Haan & Landis, 2019; Rudolph et al., 2006). Late-season mowing may make suitable milkweed available, but could also induce late-season reproduction rather than migration (Baum & Mueller, 2015).

2.2.1.3 Migration hazards

Success at monarch breeding grounds such as the Midwest did not necessarily correlate with larger numbers of monarchs in Mexico the following winter (Ries et al., 2015), nor did a larger winter cohort necessarily result in a larger population arriving at the breeding ground the following summer (Badgett & Davis, 2015). This implies that the hazards of migration could also be affecting the species (Crewe et al., 2019; Inamine et al., 2016). Research points to a decline in the first breeding generation in the southern U.S. (Flockhart et al., 2013; Inamine et al., 2016; Saunders et al., 2019). A lack of floral nectar to fuel migration (Saunders et al., 2019), habitat fragmentation or changing or more severe weather patterns may contribute to losses during migration (Agrawal & Inamine, 2018). If conditions are otherwise suitable, monarch populations then build regionally through the summer generations (Inamine et al., 2016; Ries et al., 2015).

2.2.1.4 Climate change threat

An increase in catastrophic weather events predicted by climate change, such as hurricanes in the Gulf of Mexico during migration or heat waves causing wildfires and droughts, impact monarch survival (Brower et al., 2004; Malcolm, 2018). Overwintering and breeding habitat resources may no longer be available, or suitable habitat locations may change (Aardema et al., 2011; Badgett & Davis, 2015; Batalden et al., 2007; Crewe et al., 2019; Kerr et al., 2015; Soroye et al., 2018). Altered temperature and rainfall patterns threaten the overwintering forests in Mexico (Carlón-Allende et al., 2018; Gómez-Pineda et al., 2020; Oberhauser et al., 2015; Ortiz-Bibian et al., 2017; Sáenz-Romero et al., 2012).

Climate variation may make formerly suitable areas inhospitable, as breeding season weather is associated with the size of the overwintering population (Flockhart, Brower, et al., 2017; Zalucki et al., 2015; Zylstra et al., 2021). Northward migration of milkweed may require monarchs to fly further north to reach suitable sites, especially in the first generation when their resources are at their lowest ebb (Breed et al., 2012; Lemoine, 2015; Leroux et al., 2013; Ryan et al., 2018). Monarch migration and compass are triggered by abiotic factors such as day length and temperature (Batalden et al., 2007; Guerra & Reppert, 2015). Milder winters and increased day-length further north may affect these triggers (Goehring & Oberhauser, 2002; Malcolm, 2018; Soroye et al., 2018). Reports indicate monarchs are delaying their southward migration, potentially trapping them too far north to complete migration before temperatures drop in winter (Davis & Dyer, 2015; Larrivée, 2021). The research for this thesis establishes a baseline of information about monarch distribution approaching the northern edge of its range.

Increasing temperatures may change larval growth and metabolism (Coristine et al., 2016; Zalucki, 1982). Plant phenology varies with latitude and species, suggesting a relationship with climate and location (Finch et al., 2018; Jamieson et al., 2017). The developmental stage of a plant is important for oviposition (Bergström et al., 1994; Posledovich et al., 2018). Elevated temperatures increase growth in host plants such as common milkweed (*A. syriaca*), but water stress reduces growth (Couture et al., 2015). Elevated carbon dioxide may also change the phenotype and medicinal properties of milkweed (Decker et al., 2018). Drier conditions can also reduce floral resources, especially swamp milkweed (*A. incarnata*), which requires wetlands (Malcolm, 2018; Rasmann & Pellissier, 2015).

2.2.1.5 Introduced plants

Milder North American winters and the planting of tropical milkweed such as *Asclepias curassavica*, which does not senesce, may be increasing year-round breeding and residence in monarchs in southern U.S. states such as Florida (Badgett & Davis, 2015; Howard et al., 2010; Knight & Brower, 2009). Migrating monarchs have lower rates of pathogen infection than residents, and those migrating further north are less infected (Altizer et al., 2013; Flockhart et al., 2018; Satterfield et al., 2015). Majewska et al. (2018) found that monarchs preferred plots with exotic plants, especially tropical milkweed (Corbet et al., 2001; Geest, 2017). This may be due to higher concentrations of cardenolide toxins in these plant species, which are preferred by females for oviposition (Lefèvre et al., 2012; Majewska et al., 2018).

Milder temperatures, the ‘heat island’ effect of cities with little green space, and the planting of tropical milkweeds and other nectaring plants that keep blooming until the first frost may be trapping monarchs into postponing migration until too late to reach the overwintering grounds (Brown & Hall, 2018; Singer & Parmesan, 2018). Data from eButterfly and the Ontario Butterfly Atlas show that the last 5% of monarchs leaving Canada have delayed their departure by nearly a month since 2003 (Larrivée, 2021).

The invasive European swallow-worts (*Vincetoxicum nigrum* and *V. rossicum*), have spread across North America. Though monarch females will oviposit on these exotic milkweeds, the caterpillars do not survive (Casagrande & Dacey, 2014). Further, these milkweeds aggressively invade and outcompete native milkweed species (DiTommaso & Losey, 2003). On the other hand, exotic plants can also increase floral resources and insect biodiversity, and become integrated into insect diets (Aardema et al., 2011; E. S. Davis et al., 2018).

2.2.1.6 Predators and parasites

Despite the protection provided by the cardenolides in milkweed sap, monarch juveniles are attacked and parasitized by a variety of predators (Hermann et al., 2019; Malcolm, 2018; Stenoien et al., 2015; Thogmartin, Wiederholt, et al., 2017). Mortality of juveniles varies widely, but is normally 90%, (Zalucki & Kitching, 1982c). Survival rates were better in planted, natural or non-crop agricultural sites (pastures, old fields and Conservation Reserve Program land) (Nail et al., 2015). As patch size of host plants increases, so does predation, but only up to a point (Zalucki & Kitching, 1982c). Conversely, larger patch size has also been shown to increase survival (Nail et al., 2015). Medium patch size was shown to have highest predator abundance (Pitman et al., 2018), though this did not appear to change oviposition preferences. Avoiding predation may explain the females' preference for oviposition on isolated milkweed in cropland (Myers et al., 2019). Parasitism increased with decreased milkweed stems in gardens (Geest et al., 2018), and larval survival was lower with greater egg density per plant, either from competition or greater pathogen density (Lindsey et al., 2009; Nail et al., 2015; Stenoien et al., 2016). Predation was more likely to occur at night (Zalucki & Kitching, 1982c).

2.2.1.7 Roads

While road rights of way (ROW) can provide monarchs with resources, especially in otherwise urban landscapes, mortality due to road traffic during peak migration in Illinois was estimated at a half a million monarchs a week (Berenbaum, 2015; Davis et al., 2007; Malcolm, 2018; McKenna et al., 2001). The higher sodium concentrations from road runoff result in higher mortality for *A. syriaca* and other nectaring sources (Haan et al., 2012). Monarchs nectaring on roadside plants accumulate higher sodium concentrations than monarchs nectaring in prairies (Malcolm, 2018; Snell-Rood et al., 2014). Road noise was shown to increase stress in monarch caterpillars, and the implications of the resulting habituation on adults is poorly understood (A. K. Davis et al., 2018).

2.2.1.8 Captive rearing

Though popular as a pastime and in schools, captive rearing of butterflies has sparked controversy: not only do the captive-reared butterflies have a different morphology from the wild-caught monarchs (with rounder forewings, similar to non-migratory populations), those raised in captivity did not have the southern orientation required for migration (Tenger-Trolander et al., 2019). Few tagged and reared monarchs reach the overwintering site compared to wild butterflies (Davis & Dyer, 2015). However, a recent study found that captive-reared monarchs were only temporarily disoriented, and regained their southward orientation after exposure to natural light (Wilcox et al., 2021).

2.3 Canadian situation

In Canada monarch breeding distribution varies widely among years (Flockhart et al., 2019), and is determined largely by the distribution of the host milkweed (Crewe & McCracken, 2015). Monarchs are most abundant in southern Ontario and Quebec (Crolla & Lafontaine, 1996). Although the historical amount of available milkweed may have increased in these areas owing to the development of the road network and increasing agriculture, milkweed was until 2014 controlled as a noxious weed in Ontario (Crewe & McCracken, 2015). Recent research indicates milkweed may not be as limiting in the monarch's northern range (Solis-Sosa et al., 2021).

Though long-term trends in Canada show a decline (Crewe & McCracken, 2015), other research indicates that monarch numbers are not declining here as elsewhere (Badgett & Davis, 2015). This may be due to losses during migration or overwintering after leaving Canada, or climate-change induced poleward shifts in suitable habitat bringing more monarchs further north (Badgett & Davis, 2015; Crewe & McCracken, 2015; Kerr et al., 2015; Lemoine, 2015). While there is no evidence of directional shifts between breeding regions, lower precipitation and higher maximum temperatures in the northwest and northeast North America increased the relative proportion of overwintering monarchs originating from these regions (Batalden et al., 2007; Flockhart, Brower, et al., 2017). Davis (2012), suggests the population may be able to rebound in the summer breeding range if conditions are favourable. If climate change shifts monarchs northward, extending the distance of their return migration, eastern Canada's importance to preserving monarch migration may be growing.

Eastern Ontario's undisturbed, forested land covers increase towards the north, and the study area includes remnant prairie, conserved former agricultural fields, intensive and low-intensity agricultural lands as well as extensive urban areas with investment in urban gardens and natural spaces (Baldwin et al., 2000). This study compares how monarchs react to these land covers and habitats in south and eastern Ontario, in order to aid conservation of the species and its migration.

2.4 Recovery efforts

The decline of monarch butterflies has sparked a massive and diversified effort to conserve monarchs. The Trilateral Committee of Wildlife and Ecosystem Conservation and Management, an organ of the U.S.–Mexico–Canada Agreement (USMCA), brings representatives together for monarch conservation (Geest et al., 2018; Shahani et al., 2015). States, municipalities, community associations, educational institutions and individuals on the migration pathway have all initiated efforts, such as Monarch Waystations, the Monarch Larva Monitoring Project, Milkweeds for Monarchs, the Mayor's Monarch Pledge and the Million Pollinator Garden Challenge, to conserve the species (Albrecht et al., 2007; Hellerstein et al., 2017; Oberhauser & Prysby, 2008; Shahani et al., 2015).

Research suggests a five-fold increase in the 2014–15 population size will be required to halve the quasi-extinction risk for the eastern migratory monarch population (Semmens et al., 2016). Conservation efforts across the full monarch range may be the most effective (Oberhauser et al., 2017).

2.4.1 Overwintering

The Mexican government has created the Monarch Butterfly Biosphere Reserve to protect the monarch's wintering habitat. Conservation groups and other entities work to conserve or expand overwintering habitat (Honey-Rosés et al., 2018; Manzo-Delgado et al., 2014). For example, Wildlife Without Borders partnered with the non-governmental organization ALTERNARE, located in the biosphere region, to train communities to manage resources and implement economic alternatives to reduce deforestation (U.S. Fish and Wildlife Service [USFWS] & The Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES]).

2.4.2 Habitat restoration: the hare's corner

Increasing or restoring habitat decreases extinction risks (Fernández-Chacón et al., 2014; Pitman et al., 2018). In Canada, habitat restoration should focus on productive habitats in southern Ontario where monarchs occur annually and are likely to contribute most to sustaining monarch viability (Flockhart et al., 2019). Promoting milkweed and other nectaring sources should improve conservation efforts by providing resources for larvae and adults (Inamine et al., 2016; Kral-O'Brien et al., 2020). Restoration can include planting milkweed and nectar plants across a range of locations, such as residential areas, city parks, urban spaces, powerline corridors, ROW, road medians and interchanges, as well as pollinator-friendly mowing practices (Albrecht et al., 2007). Over 1.8 billion more milkweed stems are calculated to be needed in the Midwest to restore habitat to reach viable overwintering densities of 126.6 million butterflies occupying 6 ha of overwintering habitat, a situation that calls for 'all hands on deck' (Bradbury et al., 2017; Malcolm, 2018; Pleasants et al., 2017; Thogmartin, Diffendorfer, et al., 2017; Thogmartin, López-Hoffman, et al., 2017). The largest gains in potential mean milkweed density were in protected grasslands and ROW, followed by setting aside marginal agricultural lands and urban sectors (Albrecht et al., 2007). In the Midwest, Thogmartin, López-Hoffman, et al. (2017) found that marginal agricultural land was most important, with 70% of potential habitats.

Setting aside marginal terrain unsuitable for productive agriculture--the 'hare's corner', as pollinator habitat would benefit not only monarchs and other wild species, but provide pollination and biological control to the farming system, and enhance resistance to invasion (Albrecht et al., 2007; Byun et al., 2020; Deguines, 2012; Stenoien et al., 2016). Conserving hedgerows and smaller fields with minimal human disturbance, or offering habitat exchanges is recommended (Alcock et al., 2016; Kati et al., 2012; Martin et al., 2021; Mokany et al., 2020;

Thogmartin, López-Hoffman, et al., 2017). Nectaring plants could be added to forage crops, and pollinator-friendly mowing practices, which attempt to limit mowing or time it with monarch reproduction, are recommended (Fischer et al., 2015; Pywell et al., 2011; Zalucki et al., 2016).

Groups such as the Canadian Wildlife Federation and the Habitat Working Group are working with hydro, county and municipalities to build pollinator habitat along road, hydro and pipeline ROW (Albrecht et al., 2007; Canadian Wildlife Federation [CWF], 2021).

Projects to encourage planting milkweed and other nectaring plants in urban spaces and residential homes have been enthusiastically embraced (Geest, 2017; Stenoien et al., 2015). Citizens effectively forestalled development on garden sites by portraying the gardens' value to the neighbourhood, and how their loss affected individuals (Martinez, 2009). Homeowners are converting their lawns to prairie, and municipalities are rewilding city parks, unused urban spaces and ROW (Albrecht et al., 2007; Green et al., 2016). Scaling up to encourage collections of wildlife-friendly gardens may help retain viable populations (Goddard et al., 2010). However increasing biodiversity may take longer than gardeners' time or spatial scale (Gaston et al., 2005).

2.5 Monitoring of monarchs through community science

Increasingly, long-term monitoring of biodiversity--and monarchs specifically, relies on data generated by community members rather than scientists (Howard, 2018; Oberhauser & Prysby, 2008; Prudic, McFarland, Oliver, et al., 2017). This growing practice allows data to be gathered on a scale beyond the reach of professionals (Kelling et al., 2013; Soroye et al., 2018). According to a 2017 US survey of hunting and fishing, 68.6 million people watch wildlife around their homes, 24 million take photos of nature, 21.3 million watch insects (Prudic, McFarland, Oliver, et al., 2017). For example, data from the online community science (CS) website eButterfly.org added distributional information for more than 80% of the butterfly species studied, and volunteers observed species approximately 35 days ahead of specialists (Soroye et al., 2018). The ability to monitor and predict changes on a global scale is developing rapidly, and will require effort only available from such datasets (Bird et al., 2014; Silvertown, 2009). Coupled with the growing ability to assemble and manage the large amounts of data faster than traditional scientific methods, community science has the potential to revolutionize conservation practices (Prudic, McFarland, Oliver, et al., 2017; Soroye et al., 2018). Further, as habitat is lost to development, engaging property owners in conservation and restoration is becoming a priority (Cooper et al., 2007; Tulloch et al., 2013).

Community science uses a network of volunteers to gather data for scientific investigations designed by professional researchers. The contributors are often dispersed geographically, and the research may occur over a long time scale, such as ongoing monitoring. For example, online community science database eButterfly boasted 5500 participants, 28,000 locations, and 230,000 observations by 2017 (Prudic, McFarland, Oliver, et al., 2017). In 2011 community scientists collected over 72,000 hours of data suitable for monarch research. From 1940 to 2014, of 503 publications with new monarch research, 17% used community science data (Ries & Oberhauser, 2015).

Community science-based monarch butterfly data collection and dissemination is approaching real-time, as the leading edge of the migration is tracked across the continent (Howard, 2018). Butterflies are sensitive indicators of change in ecosystem health. Monarch research is becoming a model system for recognizing threats to insects that can provide information at both the broad spatiotemporal and fine-grain levels required for global conservation issues (Burgess et al., 2017; Flockhart et al., 2013).

As a result of such close observation, the monarch butterfly has come to be “endowed with the power to shape public conversations and potentially alter policy and practice” (Gustafsson et al., 2015). The monarch is readily recognizable and valued across physical, national and mental boundaries, animating people of all political stripes, cultures and backgrounds. Associations and government bodies at federal, state and municipal level have pledged to increase habitat. Educational and conservation programs engage people with the monarchs in their community (Thogmartin, Wiederholt, et al., 2017).

2.5.1 History

Though ‘citizens’ have been participating in ‘science’ for all of human history, it is generally agreed that the earliest of the projects currently defined as citizen/community science is the Christmas Bird Count in 1880 England. The first monarch counts began in the 1950s (Ries & Oberhauser, 2015). Haklay (2013) defines such ‘classic’ forms of CS as predating scientific participation, and consisting of a dispersed but persistent network of observers who participate as a hobby or leisure activity. A second form arises from environmental justice campaigns, where participants form a ‘bucket brigade’ to manage an environmental issue, such as habitat or species loss. Community science was seen as a way to empower environmental activism (Mueller & Tippins, 2012).

The advent of the internet, GPS devices and mobile phones has changed community science yet again, creating ‘citizen cyberscientists’ (Grey, 2009; Haklay, 2013). Haklay categorizes these efforts into volunteer computing, where unused computer power is donated to process such tasks as searching for extraterrestrial life or the folding of proteins; and volunteer thinking, where participants are asked to classify information, such as interstellar dust or the craters on Mars for the Zooniverse projects, or brain connections for Eyewire (Tinati et al., 2017).

Recent developments include ‘participatory sensing,’ where mobile phones are used to upload data from apps that sense the environment (Haklay, 2013). Projects such as Open Street Map, which asks users to contribute geographical information to publicly available maps, and iNaturalist, eBird and eButterfly, which ask contributors to upload species sightings online, represent a melding of classic community science with cyberscience (Larrivée, Prudic, McFarland, & Kerr, 2018; Nugent; Sullivan et al., 2009).

2.5.2 Community scientist characterization

In 2013, Haklay described the main factor enabling the expansion of community science as the growth in developed economies of the population of well-educated people who have standard working hours that allow for leisure time (Haklay, 2013). Community science was described as a ‘serious leisure’ activity, whose participants already have some knowledge and interest in the subject. They were defined as predominantly male, well -educated and -paid, allowing for both the time required and the resources for needed equipment. Participation varies, with 1% of the contributors, known as super-users, providing almost all of the data (Haklay, 2016; Prudic, McFarland, Oliver, et al., 2017).

In a meta-analysis of research on responsible environmental behavior, Hines et al. (1987) cite knowledge of issues, knowledge of action strategies, locus of control, attitudes, verbal commitment, and an individual's sense of responsibility as associated with responsible environmental behavior. People with more knowledge of environmental issues and/or awareness of possible actions were more likely to become involved. Having an internal locus of control indicates an individual believes they are able to effect change around them.

Hines found only weak relationships between income, education or gender and responsible environmental behavior, though youth were slightly more likely to get involved (Hines et al., 1987). Perhaps these differences with Haklay's findings are because many forms of responsible environmental behavior, such as recycling, do not require specialized equipment or knowledge. Community science contributions can often require equipment, such as a mobile phone or computer, knowledge of, for example, biology or computer programming, and access to leisure and transportation.

A subsequent analysis found that the reasons for environmental participation were difficult to quantify. While knowledge was a necessary precondition, intention, moral and social norms, a sense of responsibility or guilt, as well as the ability to accomplish the task were also important components of environmental behavior (Bamberg & Möser, 2007).

2.5.3 Entomology participation

Contributors to monarch butterfly data collection can be deeply engaged in both monarch research and the use of the resulting information (Ries & Oberhauser, 2015). Less experienced volunteers tended to be more careful and diligent in locating monarch eggs, and contributors are at least as accurate as professionals (Prysby & Oberhauser, 2004).

In contrast to Haklay's findings, Penn, Penn et al. (2018) found that older women were more drawn to butterfly conservation, though they tended to downplay their pre-existing monarch knowledge. The type of contribution varied with age, as older contributors preferred data collection on paper, and were less likely to use on-line media, such as facebook, to communicate. Participants seemed to be either collectors or conservationists: the former tended to be more involved in projects involving only their species of interest (Acorn, 2017).

2.6 Data quality and analysis

Community science-gathered data serves two masters (at least): it must attract participants to become involved in gathering the data, and this data must be attractive to scientists. These motivations can come into conflict (Dennis et al., 2017). For example, the more time and effort required by the scientific goals, the fewer contributors may be willing to become involved.

Although its use is certainly growing, as both awareness and data quality increase, there is still a gap between the amount of data gathered, and the use of it by scientists (Burgess et al., 2017; Ries & Oberhauser, 2015). This may be due to a perception that the data is flawed or difficult to analyze (Pallett & Chilvers, 2013). Data originating from community science will be more likely to be used if the project is established and on-going, and partnered with an academic institution (Burgess et al., 2017). Scientists prefer younger contributors, who have received training beforehand. Community science data is seen, not as a replacement for standardized monitoring by specialists, but another tool to expand and complement scientists own sampling (Dennis et al., 2017). In this research, community science data is used to detect trends at the regional scale, then a subset of sites is examined on the ground.

Research by Haklay et al. (2010) indicates that for volunteered geographical information used in open source mapping, for example, the gain in positional accuracy levels off or decreases after 13 contributors. This is known as the ‘Linus’ Law.’ Conversely, positional accuracy becomes very good (within 6m) if there are more than 15 contributors per square kilometer. The first five contributors provided the most improvement to the accuracy (Haklay, 2010; Haklay et al., 2010).

Haklay et al. (2010) further determined that the density of contributions can vary, so some areas contribute significantly more data. A metric may be possible that gives a sense of reliability or precision of the area data due to the number of contributions (Girres & Touya, 2010; Haklay et al., 2010). Bird et al. (2014) suggest that the sheer quantity of data may offset such described drawbacks in CS datasets as spatial variation and effort. If enough individuals are uploading data from enough areas, spatial and temporal bias is no longer an issue.

Analyzing and modelling monarch butterflies, from landscape-scale migrations to habitat preferences, phenology and population dynamics over time is challenging because these systems incorporate interactions across different scales and time frames (Grant & Bradbury, 2019; Guillera-Arroita et al., 2015; Kass et al., 2020). At the landscape scale, mapping land cover/use (LCLU) change relies on available information at a scale that may not reflect monarch land use (Moreno-Sanchez et al., 2019; Samuelson & Leadbeater, 2018). At the field scale, a tiny winged insect subject to abiotic and environmental factors, temporal generational fluctuations, host plant phenology and migration makes it difficult to obtain accurate counts (Monarch Joint Venture, 2019; Nowicki et al., 2008).

2.6.1 Statistical methods for countering community science bias

Data for a biological species or set of species is gathered to provide information about fluctuations in species number, where a species occurs or does not, and what environmental components will predict how likely the species is to be found at a certain location (Latimer et al., 2006). This allows scientists to determine such things as changes in a species' distribution or abundance, and predict how the population may be changing. Sampling biases occur when data is collected in such a way that some individuals (or some populations of individuals) are less (or more) likely to be included in the sample than others, leading to a biased estimate of the parameter of interest. Numerous contributors with varying degrees of expertise and involvement can decrease accuracy in measuring or identifying species, while biases, such as non-random distribution of sampling effort or imperfect detection, may skew results (Crall, Newman et al. 2011, Stenoien, Nail et al. 2015). In a professional dataset, scientists can simply design their sampling method to accommodate their needs and account for perceived biases, whereas CS data has already been collected, and scientists wishing to use it must include methods to control confounding sources of variation. (Hochachka, Fink et al. 2012)

Environmental covariates are factors outside the control of either the data collector or the experimental design that can impact the results. For example, monarch butterflies may be present but not flying--and thus less visible--if the weather is too hot or cold, or the wind too severe. As well, the timing of migration and reproduction events will affect detectability if sampling is done too early or too late in the season (Monarch Joint Venture, 2019). These factors affect results whether professionals or amateurs gather the data. Most statistical models can account for them, as long as data can be obtained to estimate their effects, for instance, by noting weather patterns or time of the day. For example, counting larvae and eggs instead of adult monarchs can counter detection problems, as they are unaffected by such environmental conditions (Larrivée, 2018; Monarch Joint Venture, 2019).

2.6.1.1 Varying observers' ability or efficiency

Certain types of error can be more likely within a group of observers. For example, observers describing themselves as experts or experienced will tend to mistake a common species for a rare one, while a novice will commit the opposite error: mis-identifying a rare species as a common one (Bird et al., 2014; Prudic, McFarland, Hutchinson, et al., 2017). Expert data collectors may also be less likely to find a species on an inappropriate landcover, where it is not expected, than a novice volunteer with, perhaps, fewer preconceptions.

Nevertheless, studies using data validation techniques have demonstrated that experienced volunteers and professional field workers can yield comparable results (Bonter & Cooper, 2012; Prysby & Oberhauser, 2004; Wiggins et al., 2011). There will be differences in the abilities of the volunteers, but participant training, standardization of the information, verification and filtering can address sampling error and bias in this type of data collection (Bird et al., 2014).

For instance, a common identification problem occurs when the monarch butterfly is confused with its smaller mimic, the viceroy (*Limenitis archippus*). Remedies for improper identification include adding photos for comparison. Contributors are encouraged to upload their own pictures, and these can be checked by experts. eButterfly will suggest appropriate species for comparison during the data upload (Prudic, McFarland, Hutchinson, et al., 2017).

While eButterfly was found to contribute to total and regional species richness estimates, species richness alone was not assessed as well (Bird et al., 2014; Kerr et al., 2001). Using CS data to assess the distribution of species or biodiversity change may be biased by false absences due to incomplete sampling coverage (Dennis et al., 2017). For example, small first caterpillar instars and monarch butterfly eggs can be missed or mistaken (Monarch Joint Venture, 2019). Comparing instars can be a check on this detection error: the ratio of fourth and fifth instars to eggs and early instars is known (Hochachka et al., 2012; Larrivée, 2018).

Metadata is the information on the collection of the data, and can include information about the participants. Metadata collection allows a value to be placed on the expertise of the observer, and an accuracy metric determined. It can be based on such criterion as the observers' amount of training, participation or experience (Bonter & Cooper, 2012; Wiggins et al., 2011; Yu et al., 2010), In this study, the data has been vetted by experts from Environment and Climate Change Canada, eButterfly and the Montreal Insectarium. Metadata regarding users' experience was used to limit observations, and egg counts excluded to prevent mis-identification.

2.6.1.2 Unequal sampling effort

Volunteers can vary in the amount of effort they contribute, leading to differing levels of detection. A remedy for this is to request effort information upon submission. The more time a participant spends at a location, the more individuals or species they can discover (Bird et al., 2014). It is also possible to divide the numbers of monarchs into the distance travelled (catch per unit effort) (Bray & Schramm Jr, 2001).

Another method for reducing sampling bias is 'List Length'. In this method, the relationship between effort expended in butterfly observation, whether time or distance, and the number of butterfly species observed, is determined. How long a participant spends at a location can yield a calculation of what percentage of the total number of species present they can have been expected to discover (Bird et al., 2014). Such detectability factors as observer skill, weather conditions, time-of-day and phenology can also be controlled using this method (Szabo, Vesk et al. 2011, Breed, Stichter et al. 2013, Crewe, Mitchell et al. 2019).

Volunteer participants may not bother uploading data when they find no or only common butterflies (Bonney et al., 2009). Yet many statistical methods require comparing presence with absence data. Otherwise, it is necessary to generate random comparisons--called pseudo-absences (Phillips et al., 2009). eButterfly uploads ask users to indicate whether all species observed have been listed to address this issue (Larrivée, Prudic, McFarland, & Kerr, 2018).

Dedicated individuals who upload many observations may have a consistent bias, which can influence the conclusions drawn from the resulting data. For example, an eButterfly contributor interested in rare species can upload sightings of many butterflies other than monarchs, which gives a preponderance of zero monarchs. Remedies such as down-weighing or limiting the number of contributions can also disguise what may be a real trend. As contributor effort was not always recorded in the dataset used in this study, presence and absence of monarchs was used, rather than abundance. This reduced the potential effect of unequal sampling effort, but information about population abundance was lost.

2.6.1.3 Spatial and temporal biases

Non-professional observers tend to go to places that are accessible and pleasant for their observations, or where they know they are likely to find butterflies--the ‘cottage effect’ (Lawler & O'Connor, 2004; Millar et al., 2019; Tulloch & Szabo, 2012). But these may not be the only places where monarchs can be found. Similarly, because there are more observers in cities than rural or wilderness areas, more observations occur near cities. The tendency to sample the same locations while ignoring others can lead to statistical problems. Pseudo-replication occurs when different observers upload similar data from the same location or event (Boakes et al., 2010). This gives excessive weight to the characteristics of an area in the analysis that may not be true across sampling more evenly distributed on the landscape. Biodiversity trends can differ in data-rich and data-poor areas.

Spatial autocorrelation is a related issue that occurs when observations closer in space are more similar than those farther apart, or are not independent of each other. This can be the result of underlying conditions (e.g., similar soil type) or dispersal processes. Similarly, temporal autocorrelation describes a tendency for individuals to repeat behavior that can bias results: one observer camps each year at the same location, and uploads many monarch sightings from that area. Nearby, one of the park rangers walks their dog every morning down the same lane and uploads sightings. This would weigh such locations heavily (Dormann et al., 2007; Latimer et al., 2006).

Mixed-effects or Bayesian models are a class of hierarchical models that allow both fixed and random effects, and can be used to address both non-random sampling and differing sampling efficiency in a linear or additive model (Zuur et al., 2007). This model incorporates the fixed effects, such as environmental covariates, used in linear or additive models. Then it also estimates how other ‘random’ factors might influence variability in the data. For example, it is possible to use observer identifiers from the metadata to select out differing sampling efficiency or to separate regions to account for variable amount of sampling between regions (Bird et al., 2014). Including human population density as one of the explanatory factors and smoothing this variable can account for the urban spatial bias (Flockhart et al., 2013). Greater care may be needed to account for temporal bias in a time-dependent study, as in the case of Crewe, Mitchell et al. 2019, looking at monarch migratory trends (Crewe et al., 2019). They include an effect in their calculations for the temporal autocorrelation occurring among both years and on multiple days within a year to account for these potential influences.

Bayesian models use pre-existing algorithms describing known relationships, then add a spatial or temporal correlation parameter to a species distribution to account for the uncertainty of the information (Dormann et al., 2007; Latimer et al., 2006; Wikle, 2003).

Other remedies for spatial and temporal autocorrelation include geographically-weighted regression; subdividing areas or time periods and comparing data within each segment instead of across the entire dataset. The resulting variables can then be compared with those of distant regions, which have been standardized, and are therefore now more equivalent. (Dormann et al., 2007; Latimer et al., 2006). This method can be used to add weights to metadata to account for systemic bias among contributors.

Unbiased data can also be obtained from spatially or temporally biased samples by data filtering. There are numerous methods for estimating the biased distribution and then factoring it out (Dudík et al., 2006; Kantor et al., 2021 [arXiv preprint]). Heavily sampled areas can be down-weighted (Dormann et al., 2007; Phillips et al., 2009). A step is included in the analysis allowing differing valuations to be assigned to urban areas versus wilderness areas with less sampling. These methods involve the loss of valid data, as observers tend to avoid areas where they assume or know there are no butterflies. Proximity to the populated areas such as Toronto and Ottawa meant the potential for spatial and temporal bias existed in this research dataset. Multiple observations in the same location were filtered in order to account for this possibility.

Manipulating the background data can also account for confounding variables (Phillips et al., 2009). Even though a species might be found much more widely-distributed across a landscape, suppose the majority of sampling has occurred near roads or paths? Most roads tend to be situated on high ground to avoid flooding. A model might find that the species is situated near ridges and higher ground. This is not describing the species distribution, but survey distribution. So samples must be discarded to even out their distribution, resulting in information loss, or more samples taken to account for the irregularity. If the background data contains similar biases to the target data, for example, the absences are also gleaned from ridges and higher ground, then ridges would not be found to be a characteristic unique to species distribution, allowing genuine trends of interest to appear.

Machine learning models start with no assumptions: the data drives the fit of the relationship between the predictor and response variables (Bird, Bates et al. 2014). They take a portion of the dataset and use it to determine the most likely predictor-response relationships, then test their predictive value on the rest of the dataset. Community science data can be suited for these models because they do not require that the data follow a particular pattern of probability that requires a rigid experimental design. Data is not required to be linear or smooth, allowing for gaps in sampling patterns.

Semi-parametric models fuse traditional parametric models with machine-learning techniques (Hochachka et al., 2012). For example, the Occupancy-Detection-Expertise model employs the sites' occupancy covariates, the detection covariates from the checklist, and the experience of the observer to account for many biases found in CS data (Yu et al., 2010). The Spatio-Temporal Exploratory Model (STEM) model parses the data into randomized, overlapping spatial and temporal local units, which are then modelled. The significant predictor-response relationships in each local subset are identified and modelled. Then these local datasets are compared, and the patterns are scaled up to the whole dataset (Fink et al., 2010; Hochachka et al., 2012). For example, Crewe et al. (2019) began with a Bayesian framework for modelling monarch migration and abundance, using a model called INLA. Then the results were subjected to machine language iteration.

Where prior relationships between predictor and response variables are not known, ordination can visualize and rank variation patterns between predictors. These could then form the basis for variable selection for subsequent modelling, or the ranks along the differed principal component axes can be used directly as proxy variables of more complex environmental variables. One of the benefits of this method is that the variables are inherently devoid of autocorrelation. (Legendre & Gallagher, 2001; Zuur et al., 2007). In this study, Canonical Correspondence ordination was used to delineate differences in plant communities between sites in the hot and cold spots.

2.7 Conclusion

One of the most vital challenges of the scientific community is to prevent biodiversity loss (Aardema et al., 2011). Protection of butterfly communities benefits ecosystems, and the humans who use their services (Launer & Murphy, 1994; Semmens et al., 2018; Wilson, 1992). Monarch numbers are decreasing, and efforts to identify the causes and protect vital habitat are occurring throughout this migratory species' range. Land development and management on the species' overwintering, migratory and reproductive habitat, and the depredations of climate change mean it is vital to understand what contributes to success or decline across the species' range. The butterflies' ability to seek out sites in otherwise inhospitable land cover and to survive in disturbed habitats indicates that public efforts to increase monarch habitat may yield positive results (Stenoien et al., 2015).

In the context of rapid climate change, especially in northern regions, distribution patterns of migrating species and their behavior at the northern range's edge can potentially reveal much about the current and future dynamics of a species. In Canada, where the monarch reaches its northern limit, there is evidence the region can serve as a reservoir to replenish overwintering sites, and numbers may not be following the same trends as reported elsewhere. But little is known about the monarch's distribution and habitat preferences. At the regional scale, are monarchs associated with the same land covers as elsewhere? Are certain areas or habitats favoured more than others? Is milkweed a critical factor to predict the occurrence of monarchs? What nectaring plants or habitat communities do they use this far north? This research will seek to answer these questions using data from citizen science initiatives and my own field sampling. Determining what monarchs' requirements are in this region will contribute to conservation efforts at a critical time for a species migrating through a changing landscape. It will also validate citizen science efforts to contribute to conserving the species.

3 MONARCH BUTTERFLY (Danaus plexippus) BREEDING DISTRIBUTION AND HABITAT PREFERENCES IN SOUTHEASTERN ONTARIO

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3.1 INTRODUCTION

The status of the monarch butterfly (*Danaus plexippus*), a flagship species for biodiversity conservation, has received much attention (Barkham, 2020; Gustafsson et al., 2015). The species is known for its migration from and to Mexico across the North American continent over successive generations, as well as its dependence for oviposition on milkweeds of the subfamily Asclepiadoideae: the caterpillars' only food source (Agrawal, 2017; Oberhauser & Solensky, 2004; Pleasants et al., 2017). Evidence from the monarch's overwintering ground in Mexico has shown the decline by over 84% of the migratory population in eastern North America between 1993 and 2015 (Saunders, Ries et al 2019, Brower, Taylor et al. 2012, Agrawal 2019, Rendón-Salinas, Martínez-Meza et al. 2019). Research has pointed to multiple causes of the decline, such as forest degradation in the overwintering Mexican range, changing land use that reduced the availability of milkweed in the breeding range, the use of pesticides, and severe weather events (Agrawal & Inamine, 2018; Davis & Dyer, 2015; Flockhart, Brower, et al., 2017; Malcolm, 2018; Stenoien et al., 2016; Thogmartin, Wiederholt, et al., 2017), the latter increasing in recent years.

The difficulty tracking an insect across a continent and the fact that threats can happen anywhere along the migration path (Crewe et al., 2019) make untangling the relative importance of the causes of the decline challenging (Solis-Sosa et al., 2021; Zylstra et al., 2021). Understanding population dynamics and linking trends across temporal and spatial scales (Davis et al., 2007) first require information on the distribution and habitat preferences of monarchs both locally and regionally. In Eastern Canada, although early forest clearing may have increased available habitat, monitoring over 20 years at two migratory roosting locations showed an estimated decline of 5.11%yr^{-1} across sites, but also site-specific trajectories (Crewe and McCracken 2015). At the regional level, the northeastern North American population (or north central in (Flockhart, Brower, et al., 2017)), which includes eastern Canada, has occupied a growing proportion of the monarchs arriving at the overwintering grounds, suggesting these populations could be an important reservoir to sustain overwintering dynamics when weather conditions negatively impact breeding success in other parts of the breeding range (Altizer et al., 2013; Davis, 2012; Flockhart, Brower, et al., 2017; Flockhart et al., 2019). Rapidly changing climate conditions, however, could also affect populations at the northern edge of the species' distribution, even changing migratory patterns (Aardema et al., 2011; Batalden et al., 2007; Zipkin et al., 2012), as well as monarch butterfly conservation outcomes (Thogmartin, Wiederholt et al. 2017). Still, little is known about the habitat preferences and conservation status of monarchs at the edge of their northern distribution in Canada, where developed, urban or agricultural land fades into less disturbed forested landscapes.

Fortunately, the capacity for monitoring occurrences over space and time in support of scientific inquiries and conservation efforts has recently been greatly extended by a growing number of community science initiatives encouraging volunteers to upload observations of monarch and other butterflies to online databases (Howard and Davis 2015, Prudic, McFarland et al. 2017). One of these databases, eButterfly, has added distributional information for more than 80% of the butterfly species monitored in Canada (Soroye, Ahmed et al. 2018). When records include all species of butterflies observed at a location, as with eButterfly, they can provide useful insights on the conditions associated with the presence and absence of a specific species. Using data from such community initiatives, Flockhart et al. (2019) estimated the annual mean breeding distribution in Canada to be 484 943 km^2 (min: 173 449 km$_2$; max: 1 425 835 km^2), with the area of occurrence approximately an order of magnitude larger in eastern Canada than in western Canada. They identified southeastern Ontario as a priority area for monarch conservation, given its likely significant contribution to monarch population dynamics in eastern North America.

In this study, we focus on the regional distribution of monarchs in southeastern Ontario, toward the northern edge of their breeding range. We use seventeen years of records (n=5461) from eButterfly and other community science initiatives reporting on the presence of butterfly species, as well as field sampling, to compare land covers, spatial attributes, and resource availability of butterfly records that include the monarch with records that do not. These observations offer opportunities to detect whether this migrating species has distinctive habitat preferences in its northern breeding range compared to other butterfly species. Features associated with these records, such as surrounding land covers, spatial attributes and vegetation could predict where conditions are especially suitable for monarchs (Kral, Hovick et al. 2018, Moreno-Sanchez, Raines et al. 2019) in this region. Comparing these ‘hot spots,’ or clusters of monarch observations, with areas with poorer monarch numbers (‘cold spots’) could reveal conditions important to improved conservation.

Overall, our objectives are to 1) identify land cover and spatial attributes related to monarch occurrence during their summer breeding season at the regional level, 2) identify and map clusters of sites where the probability of observing monarchs is high, i.e., 'hot spots', and compare their habitat features to those of 'cold spots' in the region, and 3) compare the milkweed and potential nectaring plant species' availability at hot and cold spots in the field.

Butterfly communities are likely influenced by both local and landscape scale effects (Davis, Debinski et al. 2007, Antonsen, Kral-O'Brien et al. 2021). Because of their dependence on milkweed for breeding, we expect monarchs to be observed less in forests than in other more open habitats, with an abundance of milkweed and nectaring species being distinctive features of hot spots (Bhowmik and Bandeen 1976, Ackerly and Vane-Wright 1984, Kral, Hovick et al. 2018, Dinsmore, Vanausdall et al. 2019, Moreno-Sanchez, Raines et al. 2019, Antonsen, Kral-O'Brien et al. 2021). Nectar sources would be particularly important to support reproduction and migration efforts (Brower, Fink et al. 2006, Inamine, Ellner et al. 2016), but much remains to be discovered about adult monarch's nectaring preferences (Lukens, Kasten et al. 2020). Here, we propose an extended list, adapted from various sources, of potential nectaring plants at northern latitudes. It is also not clear whether monarchs would show a preference for agricultural habitats (Myers et al., 2019; Pitman et al., 2018; Thogmartin, López-Hoffman, et al., 2017), given the control of milkweed which, until recently, was considered a noxious weed in Ontario (Crewe & McCracken, 2015). As well, while a larger extent of suitable land covers is likely to be found in rural rather than urban areas (Theodorou, Radzevičiūtė et al. 2020), research is still examining how the recent increase in urban pollinator gardens may change monarch outcomes in urban areas (Cutting and Tallamy 2015). Failure to observe differences in plant resources between hot and cold spots could point to the importance of factors other than plant availability in determining monarch distribution (Inamine et al., 2016; Solis-Sosa et al., 2021).

3.2 MATERIAL AND METHODS

3.2.1 Study area

The study area occupies approximately 60,000 km^2 above the north shore of Lake Ontario, in the southeastern region of the Canadian province of Ontario (Figure 1). Preliminary analysis at the scale of Canada by the Montreal Insectarium indicated a concentration of monarchs in this region (Larrivée & Drapeau Picard, 2018). The study area extends along the north shore of Lake Ontario from Hamilton east to Kingston, north to Ottawa, and west to Georgian Bay. Cities included are Toronto, south Ottawa, and Peterborough. The region comprises developed areas along the lakeshore, with rich agricultural plains and river valleys transitioning to natural terrain dominated by deciduous forest going northward. Open habitats here include conserved former agricultural land in the south, but also remnant natural prairie (Catling, 2008).

3.2.2 Monarch observations

The dataset comprised 5461 recent (2002-2018, June 15-Aug 15) community science observations of adult monarchs and larvae (4568 presence), and observations reporting butterflies, but without monarchs present (893 absence). Each record has a unique identifier, a location (WGS 84 latitude, longitude), and the date of the recording. Observations had been contributed to the databases Ontario Butterfly Atlas, eButterfly and Mission Monarch (Appendix 1) (Larrivée, Prudic, McFarland, Drapeau Picard, et al., 2018; Larrivée, Prudic, McFarland, & Kerr, 2018; MacNaughton et al., 2017). Only vetted observations were conserved. Records with location errors, as well as duplicate records (same date, time, number of individuals, longitude and latitude) were removed (Appendix 1). Only the last of a series of observations of larvae from the same observer at the same location was kept to reduce potential effort biases. Adult monarch observations prior to June 15th and after August 15th were not included to ensure that only non-migrating adults monarchs were considered. Similarly, early August high counts (+10 individuals) that could represent early migratory adults in south and eastern Ontario were removed from the analyses. As observer effort was not consistently recorded, presence/absence rather than abundance was analyzed in this study.

3.2.3 Land cover and spatial variables

The area occupied by each of ten land cover types (m^2; Figure 1), within buffers (60m radius) around each observation was extracted from the Commission for Environmental Cooperation's map, *2015 Land Cover of North America at 30 meters* (Canada Centre for Remote Sensing [CCRS] et al., 2020), a reference for this region (Grekousis et al., 2015). Buffer size was selected based on the median monarch step length (60m) as described by (Zalucki et al., 2016). The urban land cover comprises any human-built feature, including roads and trails. The spatial variable 'Distance to water' (m), extracted using the Near tool within ArcMap 10.7.1, measures Euclidean distance to the nearest water body, whereas the 'Water' land cover measures the amount of water present in the 60m-radius buffer around an observation. The geographic coordinates (latitude and longitude) of each observation were also included. Concurrent points within the buffer zones were removed to leave 2468 unique observations. Where both monarch presence and absence was recorded for the same location, only a presence observation was retained. Land covers within overlapping buffers were attributed to one observation. Land cover values were extracted using the ArcMap Tabulate area tool. A 30m processing cell size was used to match the scale of the map. This resulted, however, in some variation in the total area of land cover recorded for some observations.

3.2.4 Field sampling

We sampled 81 field locations in summer 2019 for a concurrent study on monarch breeding preferences. Eleven of these locations were from within a hot spot and 11 from a cold spot, as classified by the Getis-Ord analysis (see 3.3.5.2). All the sites in the hot, and except for two urban parks, 9 of 11 sites in the cold spot were rural. Given the small sample size, we used these observations for an exploratory assessment of whether sites classified as being within a hot versus a cold spot differed in terms of plant species richness, potential nectaring plant composition and diversity, and milkweed abundance.

Field sampling was conducted from June 15-July 6, and again August 2-17, 2019. A modified version of the Integrated Monarch Monitoring Protocol was used (Cariveau et al., 2019; Commission for Environmental Cooperation [CEC], 2017; Monarch Joint Venture, 2019) to sample plant species. Environmental variables (Appendix 11) and the presence of nearby land cover classes were noted in the field around the geographical coordinates of each observation as a coarse assessment of the mapped land covers (Appendix 9).

Plant species, including milkweed stems, were counted in 12 x 1m^2 plots, at the centre, middle and edge of the site. Nectaring plant species were identified in part from available lists (Appendix 5). As most of these lists only included native plant species, non-native plant species most commonly identified in photos of monarch observations uploaded to eButterfly were added to our nectaring species list (Moczula, et al., 2022). Also, since most reference lists for nectaring species were from lower latitudes than those of our study area, similar potential species at higher latitudes as well as other species found on northern pollinator lists were substituted or added (Appendix 6).

3.2.5 Data analysis

3.2.5.1 Regional distribution in relation to land cover and spatial variables

The relationship between adult monarch presence and absence over the study area, ten land covers and three spatial variables was assessed using generalized linear modelling and the logistic regression family in R 4.0.0 (R-core, 2020). First, land cover and spatial features were combined into basic models representing distinct habitat conditions (Table 1). Then, 61 combinations of these basic models (Appendix 2)--representing alternative hypotheses about the relative importance of land cover and spatial features for monarch occurrence--were tested within a multimodel inference framework (Burnham & Anderson, 2002; Johnson & Omland, 2004; Boisvert-Marsh, Périé, & de Blois, 2019). Second-order Akaike's information criterion (AICc), the difference between AICc of a model and the lowest AICc (ΔAICc), and Akaike weights (wi) were used to rank and select the models (Mazerolle, 2020). The model with ΔAICc = 0 was interpreted as the 'best' model within that set of models, while models with ΔAICc < 2 were considered as competing models. We interpreted the model coefficients for the explanatory variables of the models with the most support (selected and competing ones).

Table 1: The land covers and spatial variables included in the basic models used to assess the regional distribution of monarchs. Various combinations of the basic models were tested in logistic regressions.

Basic Model	Land cover or spatial variables included
FOREST	needleleaf+deciduous+mixed forest
OPEN	shrubland+grassland+wetland+barren
WATER	water
URBAN	urban

Basic Model	Land cover or spatial variables included
CROP	crop
SPATIAL	latitude+longitude+distance to water

3.2.5.2 Identifying hot and cold spots

ArcGIS' Getis-Ord hot spot analysis was used to identify spatial clusters with greater (hot spots) or lower (cold spots) likelihood of observing monarchs within the regional occurrence dataset. This analysis produces for each observation a z-score, p-value, and confidence level bin (Gi_Bin). Observations in the +/-3 bins reflect statistical significance with a 99 percent confidence level and were retained as hot (+3; 486 observations) or cold (-3; 543 observations) spots in this study (Getis & Ord, 1992). Incremental Spatial Autocorrelation was used to set a distance band, the spatial extent of the analysis neighborhood, at the first clustering peak (30km).

3.2.5.3 Hot and cold spots and land cover

The amount of each land cover found within the 60m buffer was calculated for observations within hot and cold spots as defined by the Getis-Ord analysis. The relationship between hot or cold spots and land cover was tested using generalized linear modelling and logistic regression, within a multimodel inference framework as before (Table 1), excluding the spatial variables.

3.2.5.4 Hot and cold spots and vegetation attributes

Milkweed/m^2, nectaring plant Shannon diversity, and plant species richness in the hot and cold spots were compared for field sites using logistic regression in a generalized linear model.

A canonical correspondence analysis (CCA) was conducted using the vegan 2.5 package in R (Oksanen et al., 2019), constraining nectaring plant and milkweed abundance by hot and cold spots to test whether they differed in terms of plant species composition.

3.3 RESULTS

3.3.1 Regional distribution in relation to land cover and spatial variables

Based on multi-model inference and AICc, the 'FOREST+CROP+URBAN+SPATIAL' model was selected as the best among the candidate models (Table 2).

Table 2: Selection of the best model comparing land cover and spatial variables found in 60m buffers around observations with or without monarchs in the study area using Akaike's Information Criterion.

Coefficients	**Parameters**	**AICc**	**ΔAICc**	**AICc Weight**
FOREST+CROP+URBAN+SPATIAL	9[1]	1920.58	0.00	0.44
FOREST+URBAN+SPATIAL	8[2]	1921.19	0.61	0.77

1 The first model is the best-fitting model according to the AICc criterion
2 The others included differ from the best model by <2 (ΔAICc column)

In the best model, 'FOREST+CROP+URBAN+SPATIAL' the probability of observing the monarch decreased significantly with increasing cover of needleleaf and deciduous forests, urban, latitude, and distance to water (Table 3). The likelihood of observing monarchs increased significantly with increasing longitude (eastward: -80.112319 to -75.725786). In the competing model, 'FOREST+URBAN+SPATIAL', the variables were materially unchanged (Appendix 3). While the probability of observing monarchs increased in open natural habitats, these models did not explain much of the variance (open habitats model ranking is 44/61). Sixty-five percent of the monarch observations did not contain any open habitat values in their buffer (Appendix 8).

Table 3: Model estimates of the best model (based on AICc) comparing land cover and spatial variables found in 60m buffers around observations with or without monarchs in the study area: FOREST+CROP+URBAN+SPATIAL.

Coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept)	6.993e+01	9.447e+00	7.402	1.34e-13	***
Needle forest	-9.230e-05	3.782e-05	-2.440	0.014672	*
Deciduous forest	-7.940e-05	2.216e-05	-3.583	0.000340	***
Mixed forest	-2.130e-05	2.758e-05	-0.772	0.439897	
Crop	-3.933e-05	2.409e-05	-1.633	0.102517	
Urban	-7.447e-05	2.135e-05	-3.488	0.000486	***
Latitude	-9.303e-01	1.345e-01	-6.917	4.61e-12	***
Longitude	3.338e-01	5.746e-02	5.809	6.28e-09	***
Distance to Water	-1.823e-04	7.027e-05	-2.594	0.009481	**
Significance codes	'***' 0.001	'**' 0.01	'*' 0.05	'.' 0.1	' ' 1

3.3.2 Identifying hot and cold spots

Getis-Ord hot spot analysis of the regional dataset of 2469 monarch occurrences revealed 1029 observations classified as either hot (486) or cold (543) (Figure 1). The largest regions classified as hot included Prince Edward and Hastings county, and the Kawartha highlands on the northeastern shore of Lake Ontario.

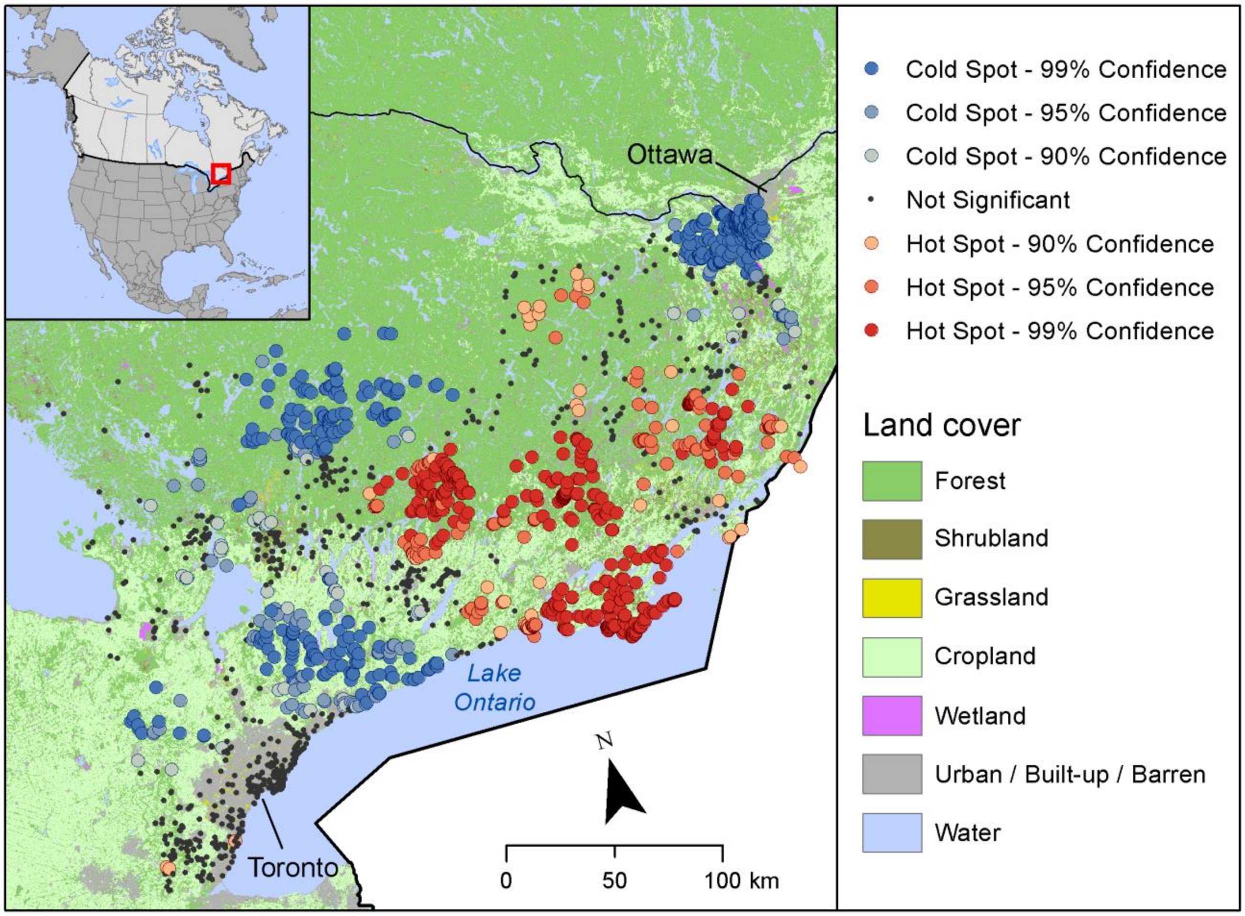

Figure 1: Ontario monarch observations, hot and cold spots. Sources: Appendix 10

3.3.3 Hot and cold spots and land cover

In the best model, 'FOREST+OPEN+URBAN' in multi-model inference (Table 4), the probability of an observation being in a hot spot increased significantly as shrubland cover increased, and declined significantly as deciduous forest and urban land cover increased (Table 5).

Table 4: Selection of the best model comparing land covers found in 60m buffers around observations in hot and cold spots using Akaike's Information Criterion.

Coefficients	Parameters	AICc	ΔAICc	AICc Weight
FOREST+OPEN+URBAN[1]	9	1386.64	0.00	0.50
FOREST+OPEN+CROP+URBAN[2]	10	1388.55	1.91	0.19

[1] The first model is the best-fitting model according to the AICc criterion.
[2] The others included differ from the best model by <2 (ΔAICc column).

Table 5: Model estimates of the best model (based on AICc) comparing land covers found in 60m buffers around observations in hot and cold spots : FOREST+OPEN+URBAN.

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	1.574e-01	1.594e-01	0.988	0.32334	
Needle forest	3.348e-05	4.004e-05	0.836	0.40306	
Deciduous forest	-9.607e-05	2.321e-05	-4.140	3.48e-05	***
Mixed forest	4.159e-05	2.749e-05	1.513	0.13024	
Shrubland	1.170e-04	3.977e-05	2.942	0.00326	**
Grassland	-7.624e-05	6.343e-05	-1.202	0.22935	
Wetland	3.835e-05	4.490e-05	0.854	0.39310	
Barrenland	-4.364e-06	3.923e-05	-0.111	0.91142	
Urban	-7.378e-05	2.464e-05	-2.994	0.00275	**
Significance codes	'***' 0.001	'**' 0.01	'*' 0.05	'.' 0.1	' ' 1

In competing model 'FOREST+OPEN+CROP+URBAN,' there was no change in the significant covers (Appendix 4).

3.3.4 Hot and cold spots and vegetation attributes

Field sites located in hot and cold regions did not differ significantly in terms of milkweed density, diversity of nectaring species and richness of plant species (Table 6). Mean density for sites in hot spots was 1.20 milkweed/m^2, and 0.76 milkweed/m^2 for cold spot sites.

Table 6: Model estimates of a logistic regression comparing vegetation attributes from field data at hot and cold spots. A positive relationship indicates the probability of being in a hot spot increases as the coefficient estimate increases.

Coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept)	-3.08884	2.41686	-1.278	0.201	
Milkweed/m^2	0.45233	0.63216	0.716	0.474	
Nectar plant diversity	1.94532	0.270	1.104	0.270	
Plant richness	-0.01208	0.14563	-0.083	0.934	
Significance codes	‘***’ 0.001	‘**’ 0.01	‘*’ 0.05	‘.’ 0.1	‘ ’ 1

3.3.5 Ordination

The first axis (CCA1) of the constrained ordination (Figure 2) separating the nectaring plant species of hot and cold spots (Appendix 5) was tested by permutation (999) and found to be significant (ANOVA, pseudo-$F(1) = 2.0933$, $p = 0.001$). The distribution and abundance of nectaring species vary significantly within the subset of hot and cold spots that were sampled, but this variation explained a small fraction (4.95%) of the site status. The vertical axis, (CA1) explained the most variation in species composition and abundance among the unconstrained axes (6.78%).

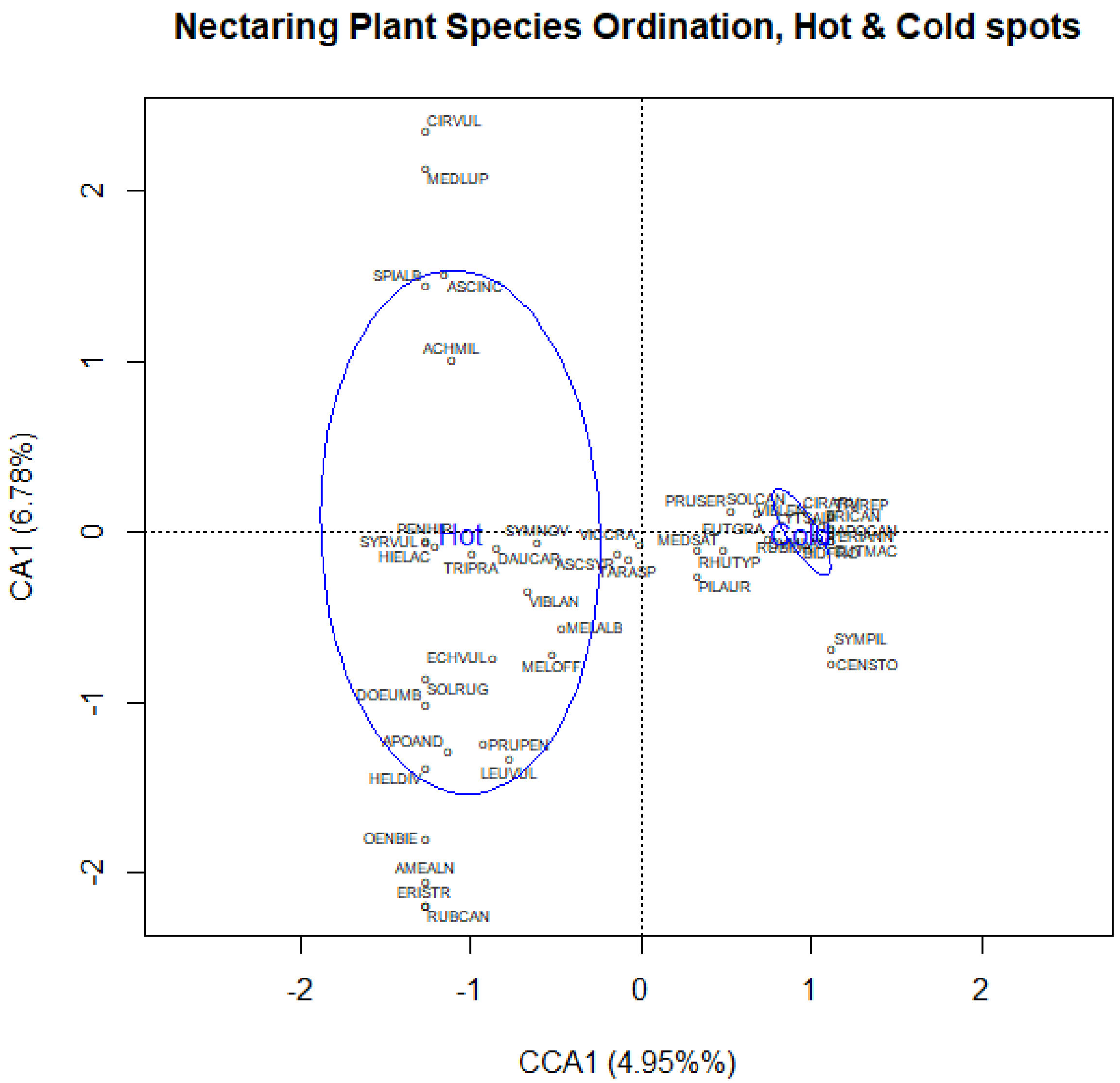

Figure 2: Ordination of nectaring plant species at 22 locations, constrained between hot and cold spots.

The small size of the confidence ellipse around the cold spot depicts the low variability in the species composition of plant assemblages found among cold sites. Conversely, the larger size of the hot spot ellipse indicates that species assemblages tended to differ more among hot spots.

The lack of overlap between the ellipses for hot and cold spots suggests that plant assemblages in the two spots were distinct, though several species found near the axes' center may be shared, such as common milkweed (*Asclepias syriaca* (ASCSYR)), vetch (*Vicia cracca* (VICCRA)) and dandelion *(Taraxacum sp.* (TARASP)). Some species found near the centroid of the cold spot, such as purple loosestrife (*Lythrum salicaria* (LYTSAL)) and spotted Joe Pye weed (*Eutrochium maculatum* (EUTMAC))*,* are associated with wet habitats, and several are intolerant of drought (Appendix 7). The greater heterogeneity of the hotspot is distributed in two groups along the vertical, unconstrained axis (CA1). Some of the species found high on this axis are associated with open field or upland habitat, such as common yarrow (*Achillea millefolium* (ACHMIL)), bull thistle *(Cirsium vulgare* (CIRVUL)) and black medic (*Medicago lupulina* (MEDLUP)). These habitats were more common in the southern, developed region of the study area (Figure 1). The species found low on the vertical axis associated with the hot spot include most of the woody species; almost all are associated with edge or successional habitats, including Canada blackberry (*Rubus Canadensis* (RUBCAN)), pin cherry (*Prunus pensylvanica* (PRUPEN)), shadbush (*Amelanchier* (AMELSP)), spreading dogbane (*Apocynum androsaemifolium* (APOAND)), and woodland sunflower (*Helianthus divaricatus* (HELDIV)). These species tended to be found on rights of ways in less disturbed sites to the north (Appendix 11).

3.4 DISCUSSION

Our results show that monarch breeding hot spots in our study area are more often associated with shrubland. The overall presence of monarchs in their summer breeding grounds of southeastern Ontario is negatively associated with increasing cover of deciduous and needleleaf forests, as well as increasing cover of urban features. Interestingly, milkweed abundance was not significantly higher in hot spots when compared to cold spots, and nectaring species richness did not differ significantly between hot and cold spots either. However, plant species composition did differ between hot and cold spots. Hot spots captured a broader habitat gradient than cold spots, the latter consisting mostly of the same plant species across the sampled field sites.

The study region is dominated by forest and agricultural land (Figure 1). As such, land covers associated with monarch occurrences are expected to reflect the availability of breeding and feeding habitats for the northeastern migratory population of monarchs, towards the northern edge of its range. We expected monarchs to be associated with low forest cover because milkweed, the preferred host plant, and many nectaring plants are species of open or edge habitats (Bhowmik and Bandeen 1976, Ackerly and Vane-Wright 1984, Oberhauser and Kuda 1987). The presence of nectaring species associated with grasslands was expected for hot spots, but the compositional gradient also included woody species of shrubland or forest edges, which supports our finding of a positive association with shrubland in hot spots. This suggests a preference for a successional stage (Steffan-Dewenter and Tscharntke 1997), or possibly the availability of alternative nectaring, or other habitat, resources in this largely forested northern region (Koh and Sodhi 2004, Davis, Debinski et al. 2007, Bergman, Dániel-Ferreira et al. 2018). Across eastern North America, Flockhart et al. (2013), using presence data, found that monarch yearly breeding occurrence was best modelled by geographical (latitude, longitude) and climatic variables, with land cover (mostly % tree and % herbaceous cover) having a lesser influence at that broad spatial scale. At the regional level, we found that geographical limits still set boundaries to monarch distribution, with the probability of monarch presence significantly decreasing northward and westward. Forest cover also increases northward in this region, which may explain, in part, the latitudinal effect. However, forest cover also increases going eastward, and they are the most abundant covers in the buffers surrounding monarch observations (Appendix 8). Based on pollen and nectar availability, the USDA (United States Department of Agriculture) derived suitability indices for various land covers for honeybees and other pollinators (Hellerstein et al., 2017; Moreno-Sanchez et al., 2019), and identified grassland, forest, and rural roadsides as the most conducive to foraging. Some forest cover may be suitable for butterflies (Bergman et al., 2018; Koh & Sodhi, 2004), and monarchs can use a variety of habitats across their breeding range (Dilts et al., 2019; Zalucki & Rochester, 2004). However, our study suggests that increasing forest cover without the presence of shrubby or edge habitats will not be conducive to monarch presence (Dinsmore et al., 2019).

Conversely, open, natural habitats, such as grassland or wetland, were expected to be significant in our study area for the monarch. But they would also have been suitable for other butterfly species found at sites where there were no monarchs. Furthermore, each of these open land covers occupy a smaller proportion of the sampled buffers than forests or urban features (Appendix 8), and their distribution can be patchy. Given the spatial configuration of these open habitats, and the spatial resolution (30m) of the land cover map we used, we may have failed to capture some of the smaller habitat patches. Indeed, although an overall accuracy of 79.90% was reported for the map we used (CCRS, 2020), our field observations suggest that small patches of open land cover in the field were not always captured by the map (Appendix 9). This was particularly the case for open habitats such as wetland, grassland, shrubland and barrenland compared to urban, forest or crop covers. Land cover datasets offering a finer resolution could provide a better assessment of habitat suitability for a species like the monarch, but may not cover the whole extent of a large study area (Samuelson and Leadbeater 2018, Moreno-Sanchez, Raines et al. 2019). Furthermore, given the various data sources used to record observations and the variation in the total amount of land cover for some observations, more data processing prior to analysis could improve the quality of the dataset. Regardless of these issues, and possibly because we were comparing butterfly habitats in a northern landscape, forest cover was more of a discriminating feature than open, natural land covers were.

The more urban an area, the less likely you are to observe monarchs in this region, supporting previous research on butterflies and urban land cover (Stenoien et al., 2015; Theodorou et al., 2020). The city of Toronto is a large metropolis situated on the north shore of Lake Ontario, just south and west of the cold and hot spots identified here. Though previous research and this study's findings would expect this large urban center to be largely 'cold', the hot spot analysis rather designates Toronto as a neutral zone. It is possible that factors acting at the macroscale, such as dominant winds (Stefanescu et al., 2007), or the proximity of a large body of water like Lake Ontario (Urquhart, 1960), could in part determine where the species will rest, feed and reproduce. Monarchs congregate in roost sites along the north coast of Lake Ontario on the flyway for the southward migration (Crolla & Lafontaine, 1996). The city of Toronto lies along this migration corridor. On their northward leg, monarchs must also pass through Toronto to reach the cold and then the hot spots (Crewe & McCracken, 2015; Miller et al., 2012). The necessity of crossing this urban landscape and the presence of monarch-friendly urban gardens and parks along the way could explain why Toronto is not a cold spot. This emphasizes the importance of providing and connecting suitable habitat patches for monarchs in an urban area on a known flyway (Dennis et al., 2013).

Cropland was not a significant cover in this research. This may be due to changing agricultural practices reducing suitable butterfly habitat, or the cover did not discriminate between the monarch and other butterflies. In forested or agricultural landscapes, ROWs can provide suitable habitat for butterflies (Cariveau et al., 2020) if properly managed, with the added benefit of increased connectivity for a migrating species (Dennis et al., 2013; Grant et al., 2018). That function is dependent on the spatial context. For instance, a ROW adjacent to a large highway with heavy, rapid traffic causing high monarch mortality (McKenna et al., 2001) does not offer the same benefits as a narrower path adjacent to a forest edge (Bergman et al., 2018; Kati et al., 2012). A hedgerow adjacent to farmland that is intensively cultivated provides less milkweed than one adjacent to a pasture or smaller field (Martin et al., 2021).

Among the spatial variables tested, the proximity of a water body was more significant for monarch occurrence than the area occupied by water near an observation point. Accessibility to water in the surrounding landscape may be important for this migrating species, but too much open water at a site will obviously replace valuable foraging resources. Combined with their preference for shrubland cover, this may indicate the importance of cooler temperatures or higher humidity levels found at shrubby edges to monarch habitat preferences (Bladon et al., 2020; Gupta et al., 2019; Harrap et al., 2021; James, 2016; Kati et al., 2012; Masters et al., 1988).

The likelihood of observing monarchs varied with geographic coordinates, suggesting geographic and/or physiological constraints to migration. Flockhart et al. (2019) and Larrivée and Drapeau Picard (2018) mapped potential monarch distribution and potential milkweed distribution in relation to climate in this region. Because both potential climatically-suitable monarch and milkweed distribution extended beyond the observed monarch distribution in our study area, we cannot conclude that there is a climatic limitation on the northern boundary of our observations. The increasing forest cover going northward is more likely to explain the latitudinal patterns we observed. Moreover, even if adequate plant resources were to be found going north, there may not be enough time for monarchs to distribute further northward before temperatures decrease and the southward migration is triggered (Breed et al., 2012; Davis & Dyer, 2015; Goehring & Oberhauser, 2002; Guerra & Reppert, 2013). The preference of the monarch for the eastern longitudes coincides with the hotspot. As the spring flight path would begin in the southwest and head northeast (Miller et al., 2012), monarchs would travel through the extensive developed areas around Toronto, as well as more intensively managed agricultural lands than those of the eastern region, which have more woodlots and dairy farms with smaller fields more suitable to the monarch (Law, 2021; Martin et al., 2021; Ontario Ministry of Agriculture Food and Rural Affairs [OMAFRA], 2016).

Other unexplored biotic factors could also be influencing the spatial distribution of monarchs (Flockhart, Brower, et al., 2017). For instance, at the continental scale, migrating monarchs have lower rates of pathogen infection than resident monarchs, and undisturbed and isolated natural areas may result in a reduction of predation and pathogens (Altizer et al., 2013; Mokany et al., 2020; Satterfield et al., 2015). Other cues, such as scent, may also dictate how monarchs select suitable habitats (McNeil, 2021).

Compared to the thousands of observations from the butterfly datasets, our field sampling was limited and the amount of variation explained by the ordination was small. Nevertheless, these sites provide valuable information on resource availability and composition between hot and cold breeding spots that complements the results obtained through mapping. In particular, the long gradient of potential nectaring plants characterizing hot spots in the ordination is similar to the monarch habitat heterogeneity found in Dilts et al. (2019), and suggests that adequate resources can be found in a variety of ecological conditions over the monarch’s northern range, from open grassy fields to shrubby forest edges. The association of shrub species characteristic of the forest edge to hot spots suggests that resources would be available for a potential northward range expansion into largely forested habitats with climate warming (Batalden et al., 2007; Breed et al., 2012; Lemoine, 2015; Zylstra et al., 2021). These species, however, may indicate monarchs' preference for an ecological community, rather than provide direct nectaring subsidies, as little is known about monarch nectar preferences in the North (Kral-O'Brien et al., 2020; Lukens et al., 2020). Nevertheless, the abundance and variety of nectar sources would be crucial for monarchs preparing for reproduction and migration (Thogmartin, Wiederholt, et al., 2017). Whether these resources would be adequate to sustain migrating populations for a longer journey south, or whether northern expansion would trap them in the north too late to escape the cold fall temperatures remains an important question.

3.4.1 Conservation implications

Monarchs can be successful in a variety of landscape and resource types in their breeding range, including in northern, forested landscapes, providing edge, successional, or shrubby habitats are available, and there is water nearby. As the forest cover closes down, however, suitability decreases. Abundance of milkweed was not a limiting factor when we compared it between hot and cold breeding spots, but it could be crucial during spring migration reproduction for monarch moving through urban areas.

The community science datasets we used provided evidence of uneven distribution of monarchs across a northern landscape. These datasets are instrumental in providing finer-grained information on species presence (and absence) over a large region where conservation efforts must be evaluated. Efforts to mitigate sampling bias associated with these data, such as encouraging surveys in areas with limited observations, such as the northern monarch extent, could increase the value of community science records for conservation. Climate change is occurring rapidly at northern latitudes and is expected to shift the distribution of many species northward (Boisvert-Marsh et al., 2019), including monarchs' summer breeding range (Breed et al., 2012; Lemoine, 2015). This study could help establish a baseline against which to measure distributional changes of the monarch, of its plant resources, and of its suitable (or unsuitable) land covers.

Finally, there exist few nectaring plant lists for pollinators in northern regions, so the list collated for the field surveys is a contribution to that knowledge. Of lists reporting plant communities to the south, few of those species are either present or blooming when monarchs first arrive in the study area to breed. Documenting what plant species monarchs utilize for nectar resources in northern regions could be an important step towards conservation. We consider our proposed list as 'a working hypothesis' in that direction.

4 GENERAL CONCLUSION

The monarch butterfly is one of the most iconic species of biodiversity conservation in North America. Its perilous journey across the continent, its dependence for survival on a variety of habitats, including urban areas, and its extreme vulnerability across its range make the monarch a unique object of study and fascination to scientists and community members. Community science observations are contributing to research on ecological adaptations and consequences across time and space. Summer populations in Canada are linked to winter ones in Mexico through a long chain of reproductive, dispersal and survival events that reverberate through the continent. These interconnections make it essential to know more about conditions at each step of the journey to assess and improve conservation practices.

Following a winged insect across a continent is not easy, so there remains much we do not know about the monarch. Research focused on its overwintering range to determine how the population was changing (Brower et al., 2012), and then in the Midwest (Thogmartin, López-Hoffman, et al., 2017), where agricultural practices reduced milkweed populations. Current research is also concerned with the effects of migration and climate change (Breed et al., 2012; Crewe et al., 2019; Flockhart, Brower, et al., 2017). My results add to that body of work, examining land cover and habitat preferences in natural and developed landscapes near the species' northern breeding limit. They form the first baseline for further research to examine how monarchs exploit their northern breeding grounds, and will inform future conservation management plans for monarch breeding habitat in eastern Canada.

In this thesis, I focused on monarchs in their summer range in Ontario, Canada, to characterize their patterns of habitat occupancy in relation to mapped land covers. I did so taking advantage of data (over 20,000 observations) that have been collected by thousands of community members and vetted by experts. I found that needleleaf and deciduous forests, as well as urban land covers were least likely to be associated with northeastern monarch breeding habitats, which is consistent with previous research (Ackerly & Vane-Wright, 1984; Kesler, 2019; Kral et al., 2018). Spatial attributes--southern latitudes, eastern longitudes and proximity to water--were positively associated with monarch observations. Monarch larvae are negatively affected by drought and heat (James, 2016), and humidity has been demonstrated to be important for butterflies and bumblebees (Gupta et al., 2019; Harrap et al., 2021), but little is known about the importance of water to adult monarchs. Humid grasslands in moist locations are recommended for butterflies, and may be an important feature for monarchs as well (Kati et al., 2012).

I mapped clusters of increased probability of monarch presence during their summer breeding period (hot spots), and assessed what characterized these spots: they were more likely to be found in shrubland and not in deciduous or urban land cover. Though monarchs are known to avoid forest cover (Dinsmore et al., 2019), and the literature points to a positive association with open cover and cropland (Ackerly & Vane-Wright, 1984; Kesler, 2019; Kral et al., 2018; Myers et al., 2019), there is little mention of the role of shrubland and proximity to forest cover. This landscape feature may be preferred in this northeastern part of their breeding range.

I did not detect significant difference in plant species richness, nectaring plant diversity and milkweed abundance between hot and cold spot sites. While planting more milkweed is considered an important conservation action (Thogmartin, López-Hoffman, et al., 2017), milkweed may not be limiting monarch success in this region (Solis-Sosa et al., 2021). Beyond planting milkweed, considering factors such as the amount of shrub present or proximity to water may contribute to conservation at these northern latitudes. The finding that milkweed abundance does not differ between hot and cold clusters, however, would need to be validated on a larger field sample.

Habitat characteristics showed hot spots included a larger gradient of habitats than cold spots, ranging from drier, conserved fields in the south to less disturbed forest openings in the north. This implies that monarchs' breeding hot spots expand over a variety of habitat types compared to sites found in cold clusters. Monarchs have been found to make use of diverse habitats elsewhere (Bhowmik, 1994; Dilts et al., 2019; Hartzler, 2010; Pleasants & Oberhauser, 2013; Zalucki & Rochester, 2004; Zaya et al., 2017).

Finally, establishing monarchs' presence and preferences in the northeastern part of their summer breeding range contributes to the establishment of baseline data that will be vital to further research ascertaining how monarchs respond to climate change. Microclimatic conditions determined by a shrub cover or the proximity of water may be as important as macroclimatic conditions in influencing daily movement in the landscape, especially as macroclimatic conditions, such as heat waves and droughts, become more extreme.

4.1 Recommendations

Though planting milkweed is considered one of the most effective aids to monarch recovery (Inamine et al., 2016; Kral-O'Brien et al., 2020; Thogmartin, López-Hoffman, et al., 2017), this research suggests this strategy may not be as effective in the northeastern part of their summer breeding range, outside of urban areas. Further research comparing other factors in a greater number of hot and cold spots, such as the role of abiotic factors or flight corridors, would be useful. More extensive validation and comparison of land covers found in the region, and further examination of factors such as shrubland cover and proximity to water to determine why they are attractive to monarchs is recommended. Investigating whether breeding site selection is influenced by chemical tracts left behind by breeding monarchs from the previous summer could also be informative (McNeil, 2021).

My results contribute further detail to other research recommending preserving the ‘hare’s corner’; remnant prairie, open marginal terrain, and smaller fields with minimal human disturbance as pollinator habitat. Not only could this aid in maintaining a vital reservoir for monarch recovery, but also for wild pollinators in general, allowing us to benefit from the pollination and biological control services they provide to farming systems (Albrecht et al., 2007; Alcock et al., 2016; Byun et al., 2020; Deguines, 2012; Kati et al., 2012; Martin et al., 2021; Stenoien et al., 2016; Thogmartin, López-Hoffman, et al., 2017). Ensuring management for pollinators on ROW, powerline corridors and other marginal spaces, especially in the forested landscapes of the north, may also contribute to monarch conservation (Albrecht et al., 2007; Fischer et al., 2015; Zalucki et al., 2016).

Projects to encourage planting milkweed and other nectaring plants in urban spaces and residences have been enthusiastically adopted, and may counteract the negative effects of urban development, especially if conservation is scaled-up to encourage collections of wildlife-friendly gardens (Coristine et al., 2016; Goddard et al., 2010; Green et al., 2016; Mathew & Anto, 2007). Further research to document these areas’ effectiveness, and compare this conservation strategy to preserving undisturbed habitat or promoting restoration in rural habitats is suggested (Soga et al., 2014).

The presence of woody species on nectaring plant lists in the north, which are not listed elsewhere, implies that not enough is known about nectar resources at northern latitudes. Further study to determine what resources monarchs use in spring, as they are moving towards the northern edge of their range, would be useful for the identification and management of monarch-friendly habitats and resources.

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6 APPENDICES

6.1 Appendix 1

Dataset metadata

We thank eButterfly, the Toronto Entomologists' Association, Mission Monarch, the Montreal Insectarium and all of their affiliated community scientists for collecting, reporting and vetting butterfly observation data used in this publication.

Only vetted observations were conserved (i.e., records with unlikely locations such as Nunavut, or with coordinates not fitting the location, were removed), duplicates (same date, time, number of individuals, longitude and latitudes) were deleted.

Observations used in the absence dataset confirmed they had listed all species observed.

Lat: 43.330922 to 45.413941

Long: -75.725786 to -80.112319

6.2 Appendix 2

Table A2: Land cover and spatial features model combinations tested with monarch occurrence as the response variable. FOREST includes deciduous, mixed and needleleaf forest covers. OPEN natural habitats include grassland, wetland, shrubland and barrenland, while SPATIAL includes latitude, longitude and distance to water.

FORESTS+CROP+URBAN+SPATIAL
FOREST+URBAN+SPATIAL
FOREST+URBAN+WATER+SPATIAL
FOREST+OPEN+URBAN+SPATIAL
FOREST+OPEN+CROP+URBAN+SPATIAL
URBAN+SPATIAL
FOREST+SPATIAL
FOREST+OPEN+CROP+URBAN+WATER+SPATIAL
URBAN+WATER+SPATIAL
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FOREST+OPEN
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INTERCEPT
FOREST+OPEN+CROP
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CROP
FOREST+CROP
CROP+WATER
FOREST+CROP+WATER

6.3 Appendix 3

Table A3: Model estimates of the competing model (based on AICc) comparing land cover and spatial variables found in 60m buffers around observations with or without monarchs in the study area: FOREST +URBAN+SPATIAL.

Coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept)	7.011e+01	9.432e+00	7.433	1.06e-13	***
Needle Forest	-7.496e-05	3.617e-05	-2.073	0.03822	*
Deciduous Forest	-6.386e-05	1.970e-	-3.241	0.00119	***
Mixed Forest	-6.616e-06	2.586e-05	0.256	0.79806	
Urban	-6.024e-05	1.913e-	-3.149	0.00164	**
Latitude	9.258e-01	1.341e-01	-6.905	5.03e-12	***
Longitude	3.406e-01	5.730e-02	5.945	2.76e-09	***
Distance to water	-1.993e-04	6.894e-05	-2.891	0.00384	**
Significance codes	‘***’ 0.001	‘**’ 0.01	‘*’ 0.05	‘.’ 0.1	‘ ’ 1

6.4 Appendix 4

Hot spot competing model

Table A4: Model estimates of the competing model (based on AICc) comparing land covers found in 60m buffers around observations in hot and cold spots : FOREST+OPEN+CROP+URBAN.

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	9.105e-02	2.456e-01	0.371	0.71084	
Needleleaf forest	4.000e-05	4.405e-05	0.908	0.36392	
Deciduous forest	-8.993e-05	2.892e-05	-3.110	0.00187	**
Mixed forest	4.788e-05	3.270e-05	1.464	0.14314	
Shrubland	1.232e-04	4.348e-05	2.834	0.00460	**
Grassland	-6.995e-05	6.581e-05	-1.063	0.28778	
Wetland	4.476e-05	4.841e-05	0.925	0.35516	
Barrenland	1.620e-06	4.269e-05	0.038	0.96973	
Cropland	1.039e-05	2.927e-05	0.355	0.72256	
Urban	-6.854e-05	2.872e-05	-2.386	0.01702	*
Significance codes	‘***’ 0.001	‘**’ 0.01	‘*’ 0.05	‘.’ 0.1	‘ ’ 1

6.5 Appendix 5

Table A5: Plant names (nomenclature follows VASCAN (Brouillet L 2010))

Abbreviation	Genus Species	English Common Name
ACHMIL	*Achillea millefolium* Linnaeus	common yarrow
AMEALN	*Amelanchier alnifolia (Nuttall) Nuttall ex M. Roemer*	Saskatoon
APOAND	*Apocynum androsaemifolium* Linnaeus	spreading dogbane
APOCAN	*Apocynum cannabinum* Linnaeus	hemp dogbane
ASCINC	*Asclepias incarnata* Linnaeus	swamp milkweed
ASCSYR	*Asclepias syriaca* Linnaeus	common milkweed
BIDFRO	*Bidens frondosa*	devil's beggarticks
CENSTO	*Centaurea stoebe* Linnaeus	spotted knapweed
CIRARV	*Cirsium arvense*	Canada thistle
CIRVUL	*Cirsium vulgare* (Savi) Tenore	bull thistle
DAUCAR	*Daucus carota* Linnaeus	wild carrot
DOEUMB	*Doellingeria umbellata* (Miller) Nees	flat-top white-aster
ECHVUL	*Echium vulgare* Linnaeus	common viper's-bugloss
ERIANN	*Erigeron annuus* (Linnaeus) Persoon	annual fleabane
ERICAN	*Erigeron canadensis* Linnaeus	Canada fleabane
ERISTR	*Erigeron strigosus Muhlenberg ex Willdenowspecies*	rough fleabane
EUTGRA	*Euthamia graminifolia* (Linnaeus) Nuttall	grass-leaved goldenrod
EUTMAC	*Eutrochium maculatum* (Linnaeus) E.E. Lamont	spotted Joe Pye weed
HELDIV	*Helianthus divaricatus* Linnaeus	woodland sunflower

HIELAC	*Hieracium lachenalii* Suter	common hawkweed
LEUVUL	*Leucanthemum vulgare* Lamarck	ox-eye daisy
LYTSAL	*Lythrum salicaria* Linnaeus	purple loosestrife
MEDLUP	*Medicago lupulina* Linnaeus	black medic
MEDSAT	*Medicago sativa* Linnaeus	alfalfa species
MELALB	*Melilotus albus* Medikus	white sweet-clover
MELOFF	*Melilotus officinalis* (Linnaeus) Lamarck	yellow sweet clover
OENBIE	*Oenothera biennis* Linnaeus	common evening-primrose
PENHIR	*Penstemon hirsutus* (Linnaeus) Willdenow	hairy beardtongue
PILAUR	*Pilosella aurantiaca*	orange hawkweed
PRUPEN	*Prunus pensylvanica* Linnaeus	pin or chokecherry
PRUSER	*Prunus serotina* Ehrhart	black cherry
RHUTYP	*Rhus typhina* Linnaeus	staghorn sumac
RUBCAN	*Rubus Canadensis* Linnaeus	Canada blackberry
RUBIDA	*Rubus idaeus* Linnaeus	red raspberry
SOLCAN	*Solidago canadensis/gigantea/altissima*	Canada/giant/ tall goldenrod
SOLRUG	*Solidago rugosa* Miller	rough-stemmed goldenrod
SPIALB	*Spiraea alba* Du Roi	white meadowsweet
SYMLAN	*Symphyotrichum lanceolatum* (Willdenow) G.L. Nesom	white panicled aster
SYMNOV	*Symphyotrichum novae-angliae* (Linnaeus) G.L. Nesom	New England aster

SYMPIL	*Symphyotrichum pilosum* (Willdenow) G.L. Nesom	old field aster
SYRVUL	*Syringa vulgaris* Linnaeus	common lilac
TARASP	*Taraxacum species*	dandelion species
TRIPRA	*Trifolium pretense* Linnaeus	red clover
TRIREP	*Trifolium repens* Linnaeus	white clover
VIBLAN	*Viburnum lantanoides* Michaux	hobblebush
VIBLEN	*Viburnum lentago* Linnaeus	nannyberry
VICCRA	*Vicia cracca* Linnaeus	tufted vetch

6.6 Appendix 6

Nectaring plant list sources

- Xerces society (Xerces Society, 2021)
- Monarch Joint Venture (Monarch Joint Venture, 2021)
- US Department of Agriculture (Galea et al.)
- East Georgian Bay Stewardship Council (Eastern Georgian Bay Stewardship Council & Georgian Bay Biosphere Reserve),
- Ladybird Johnson Wildflower Center (Johnson Wildflower Center, 2021)
- Credit Valley Conservation (Credit Valley Conservation)
- Wild Ones (Wild Ones)
- North American Butterfly Association (North American Butterfly Association [NABA], 1998)
- Monarch Watch (Monarch Watch, 2021)

6.7 Appendix 7

Table A7: Plant species habitats

Genus Species	English Common Name	Habitat*⁺	1st Axis	2nd Axis
Achillea millefolium Linnaeus	common yarrow	Frequently found in the mildly disturbed soil of grasslands and open forests; medium drought tolerance; both native and introduced; can be invasive; moderate shade tolerance	low hot	high
Amelanchier alnifolia (Nuttall) Nuttall ex M. Roemer	serviceberry	Native woody; edge; low drought tolerance; shade tolerant	low	low
Apocynum androsaemifolium Linnaeus	spreading dogbane	Native; upland	low hot	low
Apocynum cannabinum Linnaeus	hemp dogbane	Native, medium drought tolerance; intermediate shade tolerance	high	med
Asclepias Incarnate Linnaeus	swamp milkweed	Obligate wetland spp.; native; full sun to partial shade; host	low hot	high
Asclepias syriaca Linnaeus	common milkweed	Native; upland; host	med	med
Bidens frondosa	devil's beggarticks	Native, FACW, low drought tolerance, intermediate shade tolerance	high	med
Centaurea stoebe Linnaeus	spotted knapweed	Introduced. Nectar. In its native range grows in the forest-grassland interface on deep, well- developed to dry soils. Outside range	high	med
Cirsium arvense	Canada thistle	Invasive, FACU, wetland, upland terrestrial, nectar, anthropogenic (man-made or disturbed habitats), meadows and fields	high	med

Genus Species	English Common Name	Habitat*+	1st Axis	2nd Axis
Cirsium vulgare (Savi) Tenore	bull thistle	Introduced; FACU wetland	low	high
Daucus carota Linnaeus	wild carrot	Introduced; upland; edge	low hot	med
Doellingeria umbellata (Miller) Nees	flat-top white-aster	Native; FAC	low hot	low
Echium vulgare Linnaeus	common viper's-bugloss	Introduced. Abundant populations are found on coarse, sandy soils of limestone or dolomite parent material, although populations can also be found in areas with acidic soils and granitic parent material. It grows well on soils with poor fertility. It is a weed of sparsely vegetated and disturbed areas and typically is found in wastelands or disturbed areas, along roadsides and watercourses, and in overgrazed pastures. Blueweed does not grow well under dense vegetation.	low hot	low
Erigeron annuus (Linnaeus) Persoon	annual fleabane	Native; FACU, anthropogenic (man-made or disturbed habitats), meadows and fields	high	med
Erigeron canadensis Linnaeus	Canada fleabane	Native FACU, anthropogenic (man-made or disturbed habitats), meadows and fields	high	med
Erigeron strigosus Muhlenberg ex Willdenow	rough fleabane	Native, FACU, medium drought tolerant, shade intolerant	low	low
Euthamia graminifolia (Linnaeus)	grass-leaved goldenrod	Native, facultative wetland plant that usually occurs in wetlands (67–99%) but is occasionally found in non-wetlands.	med	med

Genus Species	**English Common Name**	**Habitat*⁺**	**1st Axis**	**2nd Axis**
Nuttall		Provides a nectar source for pollinators and is well-suited for use in pollinator restoration. Can be found in moist, open ground; meadows; prairies; roadsides; ditches; once established, can tolerate droughty conditions. It is also found in shaded wood edges or sunny fields and clearings.		
Eutrochium maculatum (Linnaeus) E.E. Lamont	spotted Joe Pye weed	Native; obligate wetland	high cold	med
Helianthus divaricatus Linnaeus	woodland sunflower	Native, dry, relatively open sites, forest edges, meadows and fields, woodlands	low hot	low
Hieracium Lachenalii Suter	common hawkweed	Introduced, anthropogenic (man-made or disturbed habitats), meadows and fields	low hot	med
Leucanthemum Vulgare Lamarck	ox-eye daisy	Native; UPL, upland; intermediate shade tolerance; medium drought tolerance	low hot	low
Lythrum Salicaria Linnaeus	purple loosestrife	Introduced; typical habitat includes cattail marshes, sedge meadows, and bogs. It also occurs along ditch, stream, and riverbanks, lake shores, and other wet areas; it grows on calcareous to acidic soils, can withstand shallow flooding, and tolerates up to 50% shade.	high cold	med
Medicago lupulina Linnaeus	black medic	Introduced; intolerant to drought and shade	low	high
Medicago sativa Linnaeus	alfalfa species	Introduced; drought tolerant but shade intolerant	med	med

Genus Species	**English Common Name**	**Habitat*⁺**	**1st Axis**	**2nd Axis**
Melilotus albus Medikus	white sweet-clover	Introduced; drought tolerant but shade intolerant	low hot	low
Melilotus officinalis (Linnaeus) Lamarck	yellow sweet clover	Introduced; drought tolerant but shade intolerant	low hot	low
Oenothera Biennis Linnaeus	common evening-primrose	Native, FACU, drought tolerance medium, shade intolerant	low	low
Penstemon hirsutus (Linnaeus) Willdenow	hairy beardtongue	Native, dry alvars, prairies, savannas, and old fields	low hot	med
Pilosella aurantiaca (Linnaeus) F.W. Schultz & Schultz Bipontinus	orange hawkweed	Introduced, anthropogenic (man-made or disturbed habitats), meadows and fields	med	med
Prunus pensylvanica Linnaeus	pin or chokecherry	Native, FACU intolerant to drought & shade	low hot	low
Prunus serotina Ehrhart	black cherry	Native, FACU, medium drought tolerance, intolerant to shade	med	med
Rhus typhina Linnaeus	staghorn sumac	Native, intermediate shade tolerance, high drought tolerance, edge, dry and poor soil, anthropogenic (man-made or disturbed habitats), forest edges, meadows and fields	med	med
Rubus Canadensis Linnaeus	Canada blackberry	Native, anthropogenic (man-made or disturbed habitats), forest edges, meadows and fields, ridges or ledges, shores of rivers or lakes, shrublands or thickets, wetland margins (edges of wetlands)	low	low

Genus Species	**English Common Name**	**Habitat*⁺**	**1st Axis**	**2nd Axis**
Rubus idaeus Linnaeus	red raspberry	Native & introduced, high drought, shade tolerant, anthropogenic (man-made or disturbed habitats), forest edges, forests, meadows and fields, shores of rivers or lakes, shrublands or thickets, swamps, wetland margins	high	med
Solidago canadensis/ gigantea/ altissima	Canada/ giant/ tall goldenrod	Native, FACU, medium drought tolerant, shade intolerant Gigantea: FACW, medium drought, shade tolerant Altissima: FACU, medium drought, shade tolerant	high	med
Solidago Rugose Miller	rough-stemmed goldenrod	Native, FAC medium drought, shade tolerant	low hot	low
Spiraea alba Du Roi	white meadow sweet	Native, FACW low drought tolerance, intermediate shade	low hot	high
Symphyotrichum lanceolatum (Willdenow) G.L. Nesom	white panicled aster	Native, FACW, anthropogenic (man-made or disturbed habitats), meadows and fields, swamps, wetland margins	high	med
Symphyotrichum novae-angliae (Linnaeus) G.L. Nesom	New England aster	Native, FACW, anthropogenic (man-made or disturbed habitats), meadows and fields	low hot	med
Symphyotrichum pilosum (Willdenow) G.L. Nesom	old field aster	Native, FACU, meadows and fields	high	low
Syringa vulgaris Linnaeus	common lilac	Introduced, medium drought, shade intermediate, anthropogenic (man-made or disturbed habitats), forest edges, meadows and fields	low hot	med

Genus Species	English Common Name	Habitat*+	1st Axis	2nd Axis
Taraxacum species	dandelion	Introduced, FACU, anthropogenic (man-made or disturbed habitats), meadows and fields, shores of rivers or lakes	med	med
Trifolium pratense Linnaeus	red clover	Introduced, FACU, low drought, shade intolerant, anthropogenic (man-made or disturbed habitats), meadows and fields, shores of rivers or lakes	low hot	med
Trifolium Repens Linnaeus	white clover	Introduced, FACU, low drought, shade intolerant	high	med
Viburnum lantanoides Michaux	hobblebush	Native, FACU medium drought tolerance, shade tolerant	low hot	med
Viburnum lentago Linnaeus	nannyberry	Native, FAC, drought intolerant, shade tolerant medium	high	med
Vicia cracca Linnaeus	tufted vetch	Introduced, drought tolerance high, shade tolerance intermediate	med	med

[*] Wetland Indicator status (from The PLANTS Database, (United States Department of Agriculture [USDA] & Natural Resources Conservation Service [NRCS], 2021))

Indicator Code	Indicator Status	Designation	Comment
OBL	Obligate Wetland	Hydrophyte	Almost always occur in wetlands
FACW	Facultative Wetland	Hydrophyte	Usually occur in wetlands, but may occur in non-wetlands
FAC	Facultative	Hydrophyte	Occur in wetlands and non-wetlands
FACU	Facultative Upland	Nonhydrophyte	Usually occur in non-wetlands, but may occur in wetlands
UPL	Obligate Upland	Nonhydrophyte	Almost never occur in wetlands

$^{+}$ Habitat References:

California Academy of Sciences, National Geographic Society. 2021. iNaturalist (https://www.inaturalist.org/, 06/09/2021). San Francisco, CA, USA

Native Plant Trust. 2021. Go Botany (https://gobotany.nativeplanttrust.org/, 06/09/2021). Framingham, Massachusetts, USA.

USDA, NRCS. 2021. The PLANTS Database (http://plants.usda.gov, 06/09/2021). National Plant Data Team, Greensboro, NC USA.

6.8 Appendix 8

Monarch observation land cover

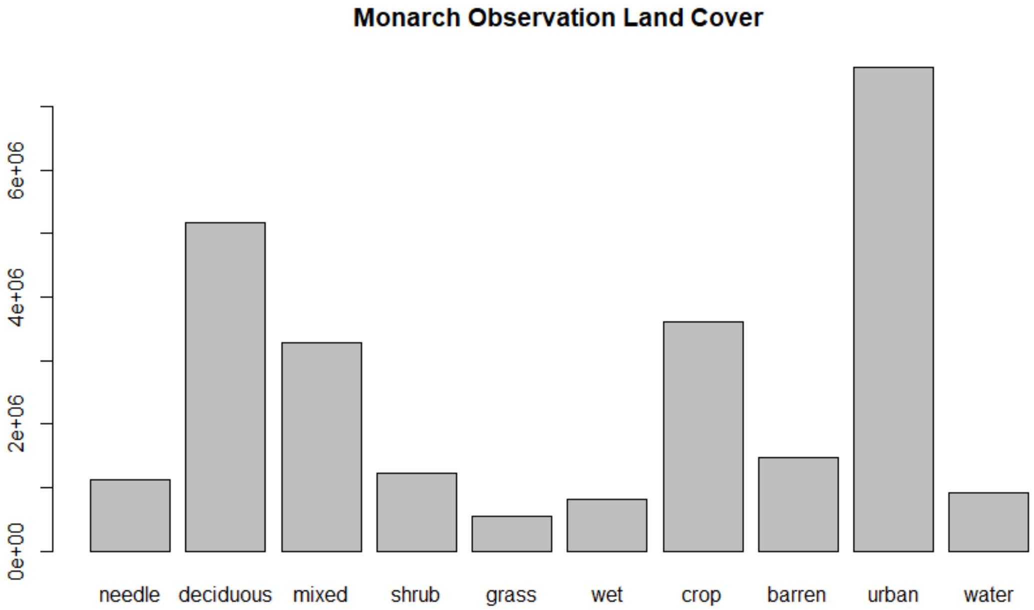

Figure A8.1: Land cover types (60m) around monarch observations.

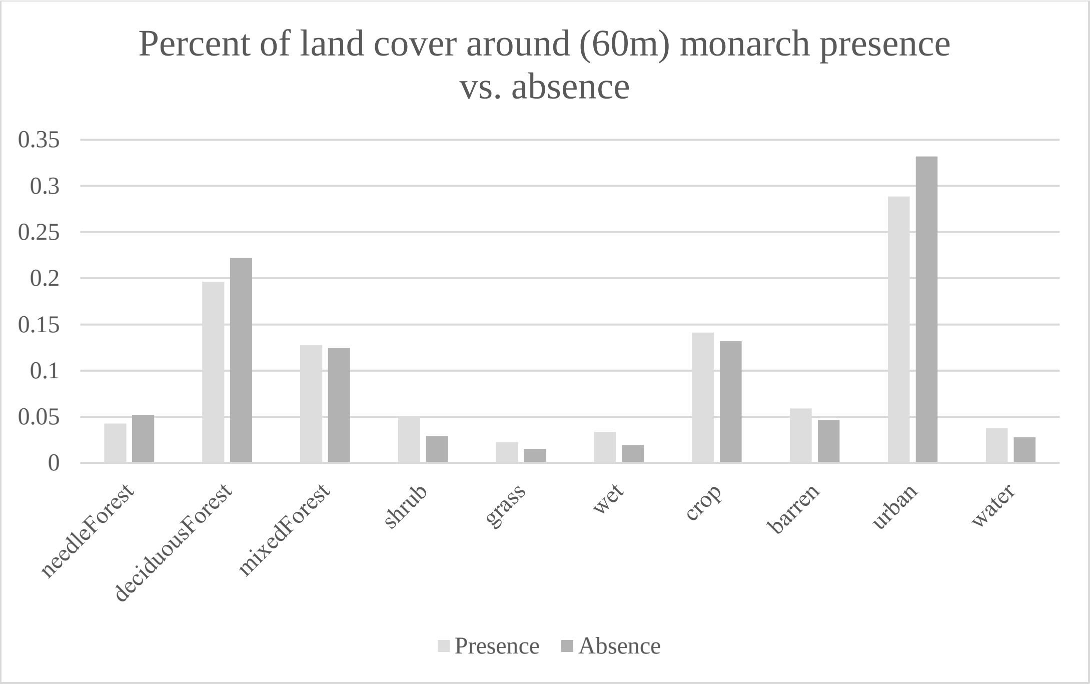

Figure A8.2: Land covers found in 60m radius around monarch observations versus observations of other butterflies.

6.9 Appendix 9

Land cover accuracy assessment

The map detected only 21% of the open habitats found in the field surveys. In an informal assessment of map accuracy, user accuracy is below 50% for all classes with the exception of grassland, urban and water. Needleleaf forests were not captured in this assessment in the field, whereas the high user's accuracy of the urban class reflects the location of many observations near roads. We were cautious in interpreting the results since the samples were not selected to represent all land cover classes, the comparison was not done pixel by pixel, and only 0.9% of sites were assessed.

Table A9: Map Accuracy: For a given class on the map, user accuracy assesses how often that class is found in the field relative to the total number of observations of that class on the map. For a given class in the field, producer's accuracy assesses how often this class is correctly mapped relative to the total number of observations in the field for that class.

Land cover/use	User accuracy	Producer accuracy
Needle forest	N/A	0%
Deciduous forest	28%	63%
Mixed forest	45%	43%
Shrubland	40%	29%
Grassland	75%	13%
Wetland*	25%	8%
Cropland	24%	100%
Barrenland	6%	33%
Urban	95%	60%
Water*	78%	28%

Land cover/use	**User accuracy**	**Producer accuracy**
Average	**42%**	**38%**

*Lake Ontario was in flood in 2019, perhaps partially explaining the greater prevalence of wetland and water observations in the field than the map.

6.10 Appendix 10

Map sources

Map created by Marian MacNair, with assistance from Patrick Kirby, Environment and Climate Change Canada.

Land cover map from Commission for Environmental Cooperation, Canada Centre for Remote Sensing (CCRS), Canada Centre for Mapping and Earth Observation (CCMEO), Natural Resources Canada (NRCan), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Comisión Nacional Forestal (CONAFOR), Instituto Nacional de Estadística y Geografía (INEGI), U.S. Geological Survey (USGS) (2020). 2015 Land Cover of North America at 30 meters. Available via: http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/ (Canada Centre for Remote Sensing [CCRS] et al., 2020)

For the inset North America map, political boundaries and waterbodies are from the North American Atlas, 2010, available via: https://open.canada.ca/data/en/dataset/491cea4e-f842-4ceb-a63d-3203ba8ec07f

6.11 Appendix 11

Table A11: Environment Variables in field sampling

Type	Measurement	Value
Soil type	% clay; semi-quantitative scale	Expected to influence vegetation patterns
Size of rights-of-way (ROW)	Absent, single-lane trail, unpaved two-lane, paved two-lane, divided highway	Expected to reflect disturbance
Latitude	WGS 1984	Expected to reflect distribution patterns
Proportion of shade, grass, forbs, shrub, trees and wetland	0%, 1-10%, 11-25%, 26-50%, >50% (of area bounded by the site edge)	Expected to reflect specific monarch site profile preferences

The envfit function was used to fit significant, uncorrelated, standardized environmental variables onto the ordination (Kral-O'Brien et al., 2020).

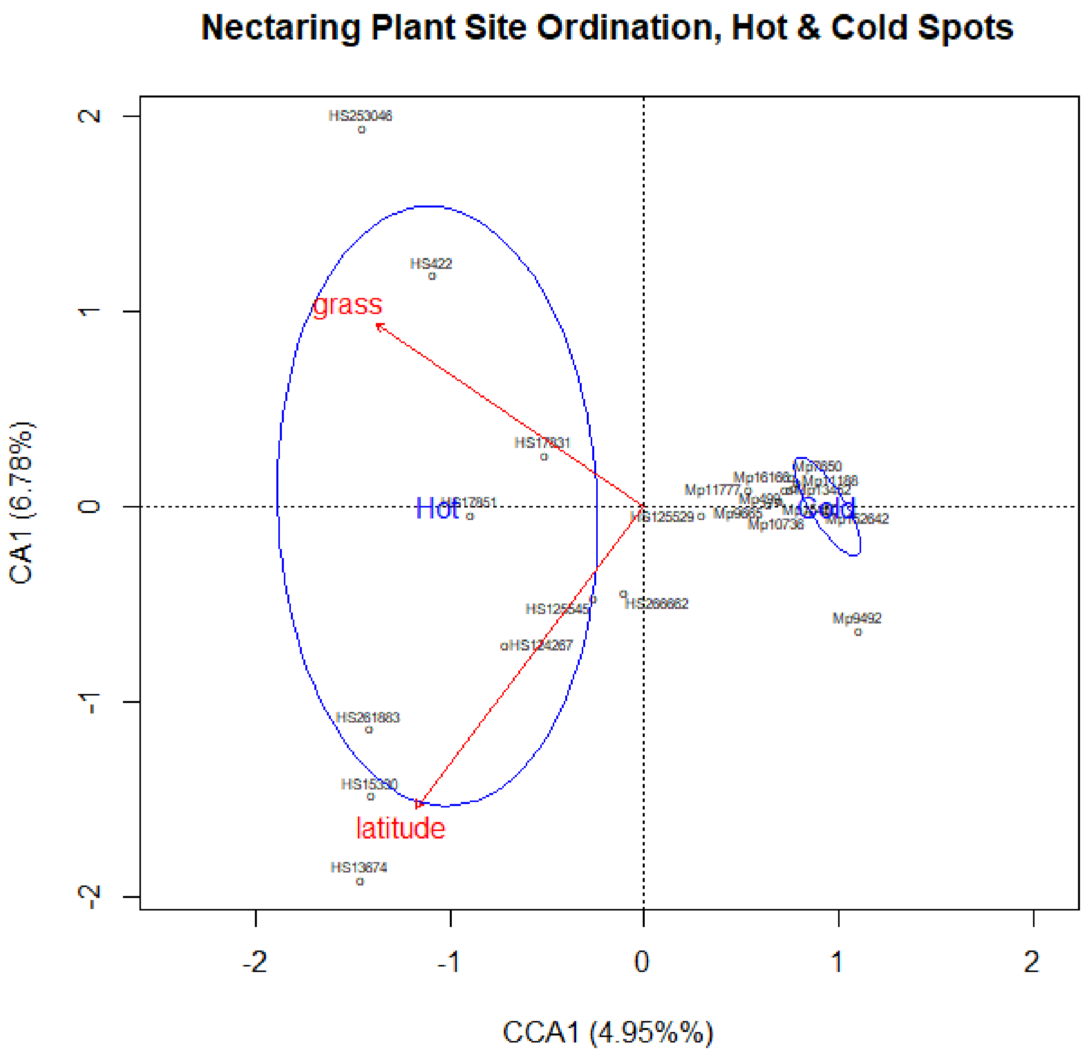

Figure A11.1: Nectaring plant site ordination, hot & cold spots, including significant fitted environmental variables and latitude.

6.12 Appendix 12

Dataset and Code upload to McGill Dataverse:

https://dataverse.scholarsportal.info/dataverse/mcgill